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Classification, Phylogeny and Zoogeographic studies of species of *Sathon* Mason (Hymenoptera: Braconidae)

by

© Daryl Joseph Michael Williams

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Entomology

EDMONTON, ALBERTA

Fall 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Classification, Phylogeny and Zoogeographic studies of species of *Sathon* Mason (Hymenoptera: Braconidae) submitted by Daryl Joseph Michael Williams in partial fulfilment of the requirements for the degree of Master of Science.

.....

Supervisor

.....

.....

Date: June 11, 1986

Abstract

The genus *Sathon* is a member of the tribe Microgastrini in the subfamily Microgastrinae of the Braconidae. Ten species are recognized in this study, occurring in the Holarctic and Neotropical regions. Five species have been described: *S. cinctiformis* Viereck 1911, *S. eugeni* Papp 1972, *S. falcatus* Nees 1834, *S. lateralis* Haliday 1834 and *S. neomexicanus* Muesebeck 1921 (1920). Five species are described as new: *S. aggeris* (type locality Quito-Baeza Rd., Ecuador), *S. circumflexus* (type locality Doolittle Ranch, Colorado), *S. laevidorsum* (type locality Cortez Pass, México), *S. masoni* (type locality Anchorage, Alaska) and *S. papilionae* (type locality Clayoquot, British Columbia). Two species groups are recognized and diagnosed, the *S. lateralis*-group containing *S. lateralis*, *S. papilionae* and *S. eugeni*, and the *S. falcatus*-group containing *S. laevidorsum*, *S. aggeris*, *S. masoni*, *S. cinctiformis*, *S. circumflexus*, *S. neomexicanus* and *S. falcatus*.

Sathon is described from characters of adult, larval and coccoon structure, distribution and phylogenetic relationships. *Sathon* species are differentiated from other members of the Microgastrini by the possession of a reduced lateral metanotal lobe, in most specimens without setae, with the phragma of the scutellum exposed. New World species of *Sathon* are described and Palaearctic species are diagnosed from the same types of features. Phylogenetic reconstruction shows that the *S. lateralis*- and *S. falcatus*-groups are monophyletic lineages recognized by differences in degree of apotypy and evolutionary trends. The pattern of relationships of *Sathon* species found shows that within the *S. lateralis*-group, *S. papilionae* and *S. eugeni* are sister species, with *S. lateralis* the sister to this sister species pair. In the *S. falcatus*-group, three species pairs are found, *S. laevidorsum* + *S. aggeris*, *S. masoni* + *S. cinctiformis* and *S. neomexicanus* + *S. falcatus*. *S. circumflexus* is the sister to *S. neomexicanus* + *S. falcatus*. *S. masoni* + *S. cinctiformis* is closer to the *S. neomexicanus* clade than *S. laevidorsum* + *S. aggeris*. Phenetic analysis yields a similar set of affinities, with differences only in the placement of *S. circumflexus* and *S. falcatus* as nearest neighbors, and of *S.*

laevidorsum + *S. aggeris* with *S. lateralis*-group species.

A short discussion of zoogeography of *Sathon* species hypothesizes one vicariance event and three long-distance dispersals combining with several unknown events to result in modern species distributions.

There are 142 figures and 4 data tables included.

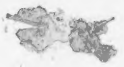

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Table of Contents

Chapter Page

Abstract iv

Acknowledgements vi

List of Tables ii

List of Figures iii

1. INTRODUCTION 1

2. MATERIALS AND METHODS 4

2.1 Materials 4

2.2 Methods 6

2.2.1 Preparation of Specimens 6

2.2.1.1 Preparation of Adults 6

2.2.1.2 Preparation of Larvae 6

2.2.2 Measurements 7

2.2.3 Illustrations 8

2.2.3.1 Drawings 8

2.2.3.2 Photomicrographs 9

2.2.4 Terms 9

2.2.5 Descriptive Format 10

2.2.6 Criteria for Species Discrimination 13

2.2.7 Criteria for Discrimination of Species Groups 13

3. TAXONOMIC TREATMENT OF THE GENUS *Sathon* 14

3.1 Classification 14

3.2 Description of *Sathon* 16

3.3 Keys to species of *Sathon* 22

3.3.1 Key to Females 22

3.3.2 Key to Known Males 24

3.4 The *S. lateralis-group* 26

3.4.1 *Sathon lateralis* Haliday 1834. 26

3.4.2 *Sathon papilionae* new species 29

3.4.3 *Sathon eugeni* Papp 1972. 32

3.5 The *S. falcatus-group* 34

3.5.1 *Sathon laevidorsum* new species 35

3.5.2 *Sathon aggeris* new species 38

3.5.3 *Sathon masoni* new species 42

3.5.4 *Sathon cinctiformis* Viereck 1911. 47

3.5.5 *Sathon circumflexus* new species 51

3.5.6 *Sathon neomexicanus* Muesebeck 1921 (1920). 55

3.5.7 *Sathon falcatus* Nees von Esenbeck 1834. 60

3.6 Taxa excluded from *Sathon* 63

4. PHYLOGENETIC RECONSTRUCTION 64

4.1 Methods 64

4.2 Characters and States 65

4.3 Reconstructed Phylogeny 76

4.3.1 Synapotypic character states 77

4.3.2 Autapotypic Character States 81

4.3.3 Homoplasy 84

4.3.4 Evolutionary Trends 87

4.3.4.1 Features of Characters and Functional Complexes 87

4.3.4.2 Features of Taxa 90

5. PHENETIC ANALYSIS 93

5.1 Methods 93

5.2 Characters 94

5.3 Phenetic Affinities 99

6. ZOOGEOGRAPHIC ANALYSIS 102

7. CONCLUSION 109

8. FIGURES 111

9. REFERENCES CITED 166

10. APPENDIX 1. TABLE OF RATIOS 173

11. APPENDIX 2. LOCALITY DATA 177

11.1 *S. eugeni* 177

11.2 *S. lateralis* 177

11.3 *S. cinctiformis* 178

11.4 *S. falcatus* 179

11.5 *S. neomexicanus* 180

12. APPENDIX 3. TAXMAP DATA FILE 186

List of Tables

Table		Page
1.	Characters and Character States used in Phylogenetic Analysis	71
2.	Characters of Table 1 displaying homoplasy in *Sathon* species	86
3.	Characters used for Taxmap analysis.	96
4.	Non-coded, morphometric characters in *Sathon* species	174

List of Figures

Figure		Page
1.	Head, dorsal aspect. Semidiagrammatic.	113
2.	Head, frontal aspect. Semidiagrammatic.	113
3.	Hind leg. Semidiagrammatic.	113
4.	Apical foretarsomeres. Semidiagrammatic.	113
5.	Apical flagellomeres. Semidiagrammatic	113
6.	Wing venation. Semidiagrammatic	113
7.	Third valvula. Semidiagrammatic.	113
8.	Pronotum of *S. lateralis*. In lateral aspect.	115
9.	Prescutellar furrow of *S. lateralis*. In dorsal aspect.	115
10.	Scutellum of *S. lateralis*. In dorsolateral aspect.	115
11.	Metapleuron of *S. lateralis*. In lateral aspect.	115
12.	Metanotum and propodeum of *S. lateralis*. In dorsal aspect.	115
13.	Anterior end of metasoma of *S. lateralis*. In dorsal aspect.	115
14.	Hind coxa of *S. lateralis*. In lateral aspect.	115
15.	Meso- and metasoma of *S. lateralis* male. In dorsal aspect	115
16.	Female genitalia of *S. lateralis*. In lateral aspect	117
17.	Oral plate of female *S. lateralis*. In anterior aspect.	117
18.	Hypopygium of *S. lateralis*. In lateral aspect.	117
19.	Head capsule of *S. lateralis* larva. In anterior aspect.	117
20.	Apex of metasoma of *S. lateralis* female. In dorsal aspect	117
21.	Male genital capsule of *S. lateralis*. In dorsal aspect.	117
22.	Male genital capsule of *S. lateralis*. In lateral aspect.	117
23.	Pronotum of *S. papilionae*. In lateral aspect.	119
24.	Prescutellar furrow of *S. papilionae*. In dorsal aspect.	119

25. Scutellum of *S. papilionae*. In dorsolateral aspect. 119
26. Metapleuron of *S. papilionae*. In lateral aspect. 119
27. Metanotum and propodeum of *S. papilionae*. In dorsal aspect. 119
28. Anterior end of metasoma of *S. papilionae*. In dorsal aspect. 119
29. Hind coxa of *S. papilionae*. In lateral aspect. 119
30. Third valvula of *S. papilionae*. High magnification displaying striate microsculpture... 119
31. Female genitalia of *S. papilionae*. In lateral aspect..... 121
32. Oral plate of *S. papilionae*. In anterior aspect..... 121
33. Hypopygium of *S. papilionae*. In lateral aspect. 121
34. Female genitalia of *S. eugeni*. In lateral aspect..... 121
35. Oral plate of female *S. eugeni*. In anterior aspect. 121
36. Hypopygium of *S. eugeni*. In anterior aspect..... 121
37. Head capsule of *S. eugeni* larva. In anterior aspect. 121
38. Pronotum of *S. eugeni*. In lateral aspect. 123
39. Prescutellar furrow of *S. eugeni*. In dorsal aspect..... 123
40. Scutellum of *S. eugeni*. In dorsolateral aspect..... 123
41. Metapleuron of *S. eugeni*. In lateral aspect. 123
42. Metanotum and propodeum of *S. eugeni*. In dorsal aspect. 123
43. Anterior end of metasoma of *S. eugeni*. In dorsal aspect. 123
44. Hind coxa of *S. eugeni*. In lateral aspect. 123
45. Pronotum of *S. laevidorsum*. In lateral aspect. 125
46. Prescutellar furrow of *S. laevidorsum*. In dorsal aspect. 125
47. Scutellum of *S. laevidorsum*. In dorsolateral aspect. 125
48. Metapleuron of *S. laevidorsum*. In lateral aspect. 125
49. Metanotum and propodeum of *S. laevidorsum*. In dorsal aspect..... 125
50. Anterior end of metasoma of *S. laevidorsum*. In dorsal aspect..... 125

51. Anterior end of metasoma of *S. laevidorsum*. In lateral aspect. 125
52. Hind coxa of *S. laevidorsum*. In lateral aspect..... 125
53. Apex of metasoma of *S. laevidorsum*. In lateral aspect..... 127
54. Anterior edge of right hind wing of *S. laevidorsum*. In anteroventral aspect..... 127
55. Metanotum and propodeum of *S. aggeris*. In dorsal aspect. 129
56. Anterior end of metasoma of *S. aggeris*. In dorsal aspect. 129
57. Anterior end of metasoma of *S. aggeris*. In lateral aspect. 129
58. Hind coxa of *S. aggeris*. In lateral aspect. 129
59. Metanotum and propodeum of *S. aggeris* male. In dorsal aspect. 129
60. Anterior end of metasoma of *S. aggeris* male. In dorsal aspect. 129
61. Pronotum of *S. aggeris*. In lateral aspect. 131
62. Prescutellar furrow of *S. aggeris*. In dorsal aspect..... 131
63. Scutellum of *S. aggeris*. In dorsolateral aspect..... 131
64. Apex of metasoma of *S. aggeris*. In lateral aspect. 133
65. Male genital capsule of *S. aggeris*. In dorsal aspect..... 133
66. Male genital capsule of *S. aggeris*. In lateral aspect..... 133
67. Anterior edge of right hind wing of *S. aggeris*. In anteroventral aspect..... 133
68. Pronotum of *S. masoni*. In lateral aspect. 135
69. Prescutellar furrow of *S. masoni*. In dorsal aspect. 135
70. Scutellum of *S. masoni*. In dorsolateral aspect. 135
71. Metapleuron of *S. masoni*. In lateral aspect. 135
72. Metanotum and propodeum of *S. masoni*. In dorsal aspect. 135
73. Anterior end of metasoma of *S. masoni*. In dorsal aspect..... 135
74. Hind coxa of *S. masoni*. In lateral aspect. 135
75. Meso- and metasoma of *S. masoni* male. In dorsal aspect..... 135
76. Female genitalia of *S. masoni*. In lateral aspect..... 137
77. Oral plate of female *S. masoni*. In anterior aspect..... 137

78. Hypopygium of *S. masoni*. In lateral aspect. 137
79. Male genital capsule of *S. masoni*. In dorsal aspect. 137
80. Male genital capsule of *S. masoni*. In lateral aspect. 137
81. Pronotum of *S. cinctiformis*. In lateral aspect. 139
82. Prescutellar furrow of *S. cinctiformis*. In dorsal aspect. 139
83. Scutellum of *S. cinctiformis*. In dorsolateral aspect. 139
84. Metapleuron of *S. cinctiformis*. In lateral aspect. 139
85. Metanotum and propodeum of *S. cinctiformis*. In dorsal aspect 139
86. Anterior end of metasoma of *S. cinctiformis*. In dorsal aspect 139
87. Hind coxa of *S. cinctiformis*. In lateral aspect 139
88. Meso- and metasoma of *S. cinctiformis* male. In dorsal aspect. 139
89. Female genitalia of *S. cinctiformis*. In lateral aspect. 141
90. Oral plate of female *S. cinctiformis*. In anterior aspect. 141
91. Hypopygium of *S. cinctiformis*. In lateral aspect. 141
92. Male genital capsule of *S. cinctiformis*. In dorsal aspect. 141
93. Male genital capsule of *S. cinctiformis*. In lateral aspect. 141
94. Pronotum of *S. circumflexus*. In lateral aspect. 143
95. Prescutellar furrow of *S. circumflexus*. In dorsal aspect. 143
96. Scutellum of *S. circumflexus*. In dorsolateral aspect. 143
97. Metapleuron of *S. circumflexus*. In lateral aspect. 143
98. Metanotum and propodeum of *S. circumflexus*. In dorsal aspect. 143
99. Anterior end of metasoma of *S. circumflexus*. In dorsal aspect. 143
100. Hind coxa of *S. circumflexus*. In lateral aspect. 143
101. Meso- and metasoma of *S. circumflexus* male. In dorsal aspect 143
102. Female genitalia of *S. circumflexus*. In lateral aspect 145
103. Oral plate of female *S. circumflexus*. In anterior aspect 145
104. Hypopygium of *S. circumflexus*. In lateral aspect. 145

105. Head of adult *S. circumflexus*. In dorsal aspect 145
106. Male genital capsule of *S. circumflexus*. In dorsal aspect. 145
107. Male genital capsule of *S. circumflexus*. In lateral aspect. 145
108. Pronotum of *S. neomexicanus*. In lateral aspect. 147
109. Prescutellar furrow of *S. neomexicanus*. In dorsal aspect 147
110. Scutellum of *S. neomexicanus*. In dorsolateral aspect 147
111. Metapleuron of *S. neomexicanus*. In lateral aspect. 147
112. Metanotum and propodeum of *S. neomexicanus*. In dorsal aspect. 147
113. Anterior end of metasoma of *S. neomexicanus*. In dorsal aspect. 147
114. Hind coxa of *S. neomexicanus*. In lateral aspect. 147
115. Meso- and metasoma of *S. neomexicanus* male. In dorsal aspect. 147
116. Female genitalia of *S. neomexicanus*. In lateral aspect. 149
117. Oral plate of female *S. neomexicanus*. In anterior aspect. 149
118. Hypopygium of *S. neomexicanus*. In lateral aspect 149
119. Head capsule of *S. neomexicanus* larva. In anterior aspect. 149
120. Male genital capsule of *S. neomexicanus*. In dorsal aspect. 149
121. Male genital capsule of *S. neomexicanus*. In lateral aspect 149
122. Pronotum of *S. falcatus*. In lateral aspect. 151
123. Prescutellar furrow of *S. falcatus*. In dorsal aspect. 151
124. Scutellum of *S. falcatus*. In dorsolateral aspect. 151
125. Metapleuron of *S. falcatus*. In lateral aspect. 151
126. Metanotum and propodeum of *S. falcatus*. In dorsal aspect. 151
127. Anterior end of metasoma of *S. falcatus*. In dorsal aspect. 151
128. Hind coxa of *S. falcatus*. In lateral aspect. 151
129. Meso- and metasoma of *S. falcatus* male. In dorsal aspect 151
130. Female genitalia of *S. falcatus*. In lateral aspect 153
131. Oral plate of female *S. falcatus*. In anterior aspect 153

132. Hypopygium of *S. falcatus*. In lateral aspect. 153
133. Head capsule of *S. falcatus* larva. In anterior aspect 153
134. Head of adult *S. falcatus*. In dorsal aspect 153
135. Male genital capsule of *S. falcatus*. In dorsal aspect. 153
136. Male genital capsule of *S. falcatus*. In lateral aspect. 153
137. Reconstructed phylogeny of *Sathon* species. 155
138. Cluster diagram of phenetic analysis of *Sathon* species. 157
139. Comparison of phenetic and phylogenetic analyses 159
140. Distribution of *S. neomexicanus*. 161
141. Distribution of American species of *Sathon* exclusive of *S. neomexicanus* 163
142. Geographical history of *Sathon* species, based on known distributions and reconstructed phylogenetic relationships 165

1. INTRODUCTION

Sathon Mason is a genus of small (3-6 mm) Braconid wasps of the subfamily Microgastrinae. The genus has not had a long history, being erected by Mason in 1981 and examined in detail for the first time here. Some of the species have been known for many years and have gone through several combinations with various genera as the classification of the Microgastrinae has changed, but have not previously been considered closely related to one another. In the most widely used classification, that of Nixon (1965), two species currently in *Sathon* were placed in the *Apanteles vitripennis*-group (Nixon 1973), three in the *A. falcatus*-group and one was not treated. It was not until Mason's (1981) reclassification that emphasis was placed on host preference and type of female genitalia and a relationship between the species of *Sathon sensu* Mason was proposed. The two species in the *A. vitripennis*-group, *S. lateralis* Haliday and *S. eugeni* Papp (= *A. fausta* Nixon 1973), were unusual in this species group in that females possess long ovipositors and sheaths, unlike the short structures of other species. Mason (1981) recognized the short ovipositor and sheath (= third valvula), along with a suite of other characters, as apotypic. *S. lateralis* and *S. eugeni*, lacking these apotypies, were removed from the *A. vitripennis*-group and placed in a different tribe, the Microgastrini, where they were united with species of the *A. falcatus*-group on the basis of apparent synapotypies in the structure of the metanotum and propodeum.

As currently constituted, the genus *Sathon* contains species whose features are unusual in the Microgastrini and convergent with states found in more apotypic tribes, such as the Cotesiini. The primary synapotypy of *Sathon* species is a reduced metanotum without setae on the lateral lobe. A secondary synapotypy is reduction of the median carina of the propodeum. *Sathon* is also unusual within the Microgastrini in host choice. Some species parasitize macrolepidopterans (eg. Noctuidae), unlike other members of the tribe. Although nothing is known about the life history of *Sathon* species and few have been reared, records indicate that they may be solitary parasitoids of microlepidopterans (Paddock 1933), or gregarious

parasitoids of macrolepidopterans (R. Oetting, pers. comm.). All records indicate emergence of parasitoid larvae from a late instar of the host larva, which implies oviposition in an early instar. Oviposition in the host egg is doubtful, at least for gregarious species. Parasitism of macrolepidopterans, nearly universal in apotypic tribes such as the Cotesiini, unknown in the Microgastrini outside of *Sathon*.

The presence of unusual apotypic features in *Sathon* species makes the genus a candidate for understanding the evolution of the entire subfamily, since major trends in evolution of the subfamily seem to have been in areas of host choice and oviposition structures and behavior (Mason 1981). *Sathon* species display host choice and structural characteristics of both of the two basic types of microgastrines, microlepidopteran-parasitizing and macrolepidopteran-parasitizing. Although no major analysis of host choice evolution in *Sathon* is presented because data are insufficient, it is hoped that this review of *Sathon* will provide a framework on which such a study can be based.

A possible secondary consideration in the study of this genus is use in biological control. The economic potential of *Sathon* species is unknown, but some species have been reared from important pest lepidopterans such as the European Pine Shoot moth, *Rhyacionia buoliana* Schiffermüller, the Wax Moth, *Galleria mellonella* (L.) and *Protagrostis obscura* Barnes and McDunnough, a noctuid pest of the bluegrass seed industry. The gregarious larval habit of some *Sathon* species offers potential of rearing the large numbers of parasitoid adults necessary for biological control.

The purpose of this project is to examine the evolution and diversity of the genus *Sathon*. American species are examined in detail, but Palaearctic species are also reviewed. I characterize the species, especially with reference to characters useful in determining relationships. I use these characters to explore the evolutionary relationships among species and to reconstruct a phylogeny. From this phylogeny I propose a species-group classification and

make brief inferences about evolutionary trends in *Sathon*. Although this study suffers from a paucity of material for some species, I also give a brief discussion of zoogeographic relationships. Keys as aids to identification are also given. Evolutionary and zoogeographical trends are briefly discussed.

2. MATERIALS AND METHODS

2.1 Materials

This study is based on examination of 902 specimens, borrowed from persons or museums listed below. Codons for museums were taken from Heppner and Lamas (1982), although some were designated by me for sources that do not appear in that publication. The codons listed here are also used in species descriptions to indicate deposition of specimens.

AEI — American Entomological Institute, 5950 Warren Road, Ann Arbor, Michigan, USA 48105 (H.K. Townes).

BMNH — Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD (T. Huddleston).

BWC — Bob Wharton Collection, Department of Entomology, Texas A&M University, College Station, Texas, USA 77843.

CAS — California Academy of Sciences, Golden Gate Park, San Francisco, California, USA 94118 (W.J. Pulawski).

CNC — Canadian National Collection, Biosystematics Research Institute, K.W. Neatby Building, Ottawa, Ontario, Canada K1A 0C6 (W.R.M. Mason).

CU — Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York, USA 14853 (Q.D. Wheeler).

DJMW — Daryl J.M. Williams Collection, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3.

FSCA Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Dolye Connor Building, Gainesville, Florida, USA (J. Wiley).

JWC James Whitfield Collection, Department of Entomology, 137 Giannini Hall, University of California, Berkeley, California, USA 94720.

LMU Der Ludwig-Maximilians Universitat, Lehrstuhl für angewandte Zoologie, Amalienstrasse 52 Gg, D-8000, München 40, West Germany (E. Haeselbarth).

NRS Naturhistoriska Riksmuseet, Sektionen för entomologi, S-104 05 Stockholm 50, Sweden (K.J. Hedqvist).

OSUC Department of Entomology, Oregon State University, Corvallis, Oregon, USA 97331 (J.D. Lattin).

RNHL Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Postbus 9517, 2300 RA Leiden, Nederland (C. van Achterberg).

SMEK Snow Museum of Entomology, Department of Entomology, University of Kansas, Lawrence, Kansas, USA 66045 (D. Wahl).

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2.2 Methods

2.2.1 Preparation of Specimens

2.2.1.1 Preparation of Adults

For observation and illustration of the oral plate and genitalia of the adult, heads and metasomas were cleared in sodium hydroxide. These body parts were easily dissected from pinned or pointed specimens, as both are narrowly joined to the mesosoma. The mesosoma is customarily glued to the pin or point. Both heads and metasomas yielded easily to pressure from an insect pin. Some specimens separated entirely from the pin or point as they were insufficiently glued to it. In these instances the entire specimen was relaxed in distilled water and the desired part removed. The remainder of the specimen was transferred to 95% ethanol, dried and remounted. Parts were cleared using standard techniques and were stored in glycerine on well slides.

2.2.1.2 Preparation of Larvae

Exuviae of last instar larvae were obtained by dissection of cocoons. A line of perforations down the longitudinal axis of a cocoon was made with an insect pin and the resulting fissure was pulled open with a pair of forceps. This action fragmented the cocoon and

loosened the meconium and exuviae in the bottom. The meconium and exuviae were removed from the bottom of the cocoon with a minuten pin mounted on a handle and moistened to cause the desired material to adhere to it. The meconium and exuviae were cleared in sodium hydroxide and a permanent slide mount in Canada Balsam was made of each exuviae after examination and drawing.

2.2.2 Measurements

In descriptions, morphometric characters are discussed as ratios with most measurements given as ranges, followed by sample means and standard deviations in brackets (table 4). However, some size comparisons are not amenable to proper measurement because of imprecision, but are still useful in discriminating species. An example of this is ovipositor length, expressed relative to the length of the hind tibia. This character is very useful in separating species, displaying slight intraspecific variation. It is very difficult to measure accurately however, since the base of the ovipositor is hidden by the hypopygium. Also, T9 of the metasoma, to which the ovipositor is attached, is tilted anteriorly in some specimens, causing retraction of the visible portion. In females with relatively short ovipositors, the difference in visible length between fully retracted and fully extended states can be half of the actual length.

For characters where relative dimensions are important, but measuring error prevents a quantitative treatment, a qualitative approximation is given. These characters are not included in table 4. If the character is important in phylogenetic reconstruction or is useful in identification, then a figure is also given. Refer to figures 1 to 7 for illustration of measurement methods.

All measurements were made with a Wild M5 stereoscopic microscope equipped with a numbered measuring bar eyepiece and a doubling lens over the objective. A camera lucida was

also installed for drawings and was not removed for measuring. All measurements were transformed into ratios of the dimensions of a structure or the size of one structure relative to another. Ranges, means and standard deviations were then calculated from the ratios. In the description of *Sathon papilionae* new species, ranges only are given. The mean and standard deviation calculated from a sample size of two were not considered useful. Each specimen was measured for every morphometric character where possible, or another specimen was substituted for any two compared measurements if not. Therefore, the sample size in any species is the same for every measurement and is reported in table 4 with measurements. Sample sizes were chosen to include the maximum range geographically and morphologically. Measurements are intended strictly for descriptive purposes. Statistical analyses were not performed.

2.2.3 Illustrations

2.2.3.1 Drawings

Line drawings were made with the aid of a microscope equipped with a camera lucida. Rough sketches were made on drawing paper and later refined and inked onto drawing film. Setae that obscured other features were omitted.

Drawings of larval head capsules were made from specimens in well slides with a Leitz Wetzlar SM-LUX transmission microscope. Heads and metasomas of adults, for oral plate and genitalia drawings, were transferred to glycerine jelly (using the formula of Pantin 1969) and arranged in the desired alignment before the jelly set. They were then drawn in the same manner as the larvae. Other drawings were made from pinned or pointed dry adult specimens. Most specimens were drawn with a Wild M5 stereocopic microscope.

For *Sathon aggeris* new species, some line drawings were taken from prints of Scanning Electron Photomicrographs (see below). Some photomicrographs obtained for this species were too poor in quality to be reproduced, since the specimen was uncoated (see below). Prints were used as templates, and drawings were traced from them and transferred to drawing film. Therefore, some illustrations that appear as photomicrographs in other species treatments are rendered as line drawings for *S. aggeris*. The holotype of *S. aggeris* and the type material of *S. laevidorsum* were not dissected. Therefore, drawings of the female genitalia were taken from point-mounted specimens.

2.2.3.2 Photomicrographs

Photomicrographs were taken with a Cambridge 250 Stereoscan Scanning Electron Microscope. Specimens were removed from their pins or points and their wings were removed and placed on a separate card. Specimens were then cleaned with detergent and ultrasonication and critical point dried. They were then mounted individually on aluminum stubs with the legs separate. Specimens of species except those of *Sathon aggeris* were coated with gold and examined with the S. E. M. The *S. aggeris* female was not so coated because it is the holotype and only known female.

2.2.4 Terms

Terms for features of the larval head capsule are taken from Čapek (1970). Terms for features of adult structures are taken from Townes (1969), except for terms for male external genitalia which were taken from Snodgrass (1941), female genitalia which were taken from Ross (1945) and wing venation which were taken from Mason (1981)[1].

[1]Mason (1981) uses the terms for wing venation proposed by Eady (1974), but has numbered the abscissae of each vein.

Some terms and abbreviations not found in the above references are defined below. Codons for the terms are given before the definitions (see also fig. 1).

POL - Posterior ocellar line is the shortest distance between the lateral (= posterior) ocelli.

LOL - Lateral ocellar line is the shortest distance between a lateral ocellus and the anterior ocellus.

OOL - Ocular Ocellar line is the shortest distance between a lateral ocellus and a compound eye margin.

AOD - Anterior ocellar diameter is the greatest diameter of the anterior ocellus.

LOD - Lateral ocellar diameter is the greatest diameter of a lateral ocellus.

Island - a small oval area of subtle sculpture on terga 3 to 7 of the metasoma, dorsad of the spiracle. The sculpture is subdued in most specimens to the point that the spot is only visible by the difference in reflectivity of glare from the surrounding tergum. This term was coined by Mason (1978), but has not been widely used.

Oral plate - a sclerite on the anterior surface of the pharynx. It is anteriorly concave, and has one pair each of dorsal and ventral arms. The ventral arms connect to either side of the epipharynx. A pair of lateral rows of oval 'windows' of thin cuticle parallel the sides of the plate. This term was coined by Williams (1985).

2.2.5 Descriptive Format

One basic sentence structure is used in all descriptions. Each sentence treats a single structure. If a structure includes more than one character useful for discrimination of species, these characters are separated by semicolons. In this way the name of the structure is repeated

as seldom as possible and there is little confusion about which structure a character is part of. Exceptions occur when the description of a character is so long, or when there are so many characters in a structure, that confusion results if the name of the structure is not repeated. Figure numbers are given in one of two places for each sentence with an accompanying figure. If the sentence includes more than one character the figure number of the structure is given immediately after the name of the structure. All character states are found on that figure. If the sentence includes only one character, the figure number is given at the end of the sentence.

The generic description serves two purposes. It characterizes *Sathon* relative to other genera in the subfamily, and displays the range of variability of characters within the genus. These functions are not discriminated in the description except in the diagnosis, which contains only characters for discrimination of *Sathon*. The list of references on *Sathon* species in the synonymy section of the generic description is not intended as a complete listing. Most references refer to Palaearctic species which are not examined in detail in this study, originally described in other, currently valid genera. Therefore, records of Palaearctic species are limited to significant taxonomic references. The reader is referred to Shenefelt (1972) for regional lists, life history references, etc. This format is also followed in diagnoses of Palaearctic species.

Characters that are invariant within *Sathon* are not repeated in species descriptions. Species descriptions characterize species relative to other *Sathon* species only. American species are fully described, but Palaearctic species have been treated four times since 1945 (Wilkinson 1945, Nixon 1965 and 1973, Papp 1983), and so are only diagnosed. These diagnoses are designed primarily for identification, and are not of the same format as full descriptions, with one exception. Characters of the female genitalia have not been adequately treated by previous authors. Given the importance of female genital characters in *Sathon* phylogeny, these characters are fully described in each diagnosis. Some characters found in Palaearctic species that do not appear in the diagnoses are noted in section 4.2 (Reconstructed Phylogeny), section 5.2 (Phenetic Analysis) and Appendix 1 (table of ratios).

Three formats are used for locality data in the descriptive section. New species have all localities listed as type material, with distributions summarized from localities listed. Previously described American species have sections for type material examined and distribution, with lists of localities personally examined given in appendix 2. Distribution data are summarized from the information in the appendix. Range maps are given for American species. For Palaearctic species, type material was not available, although specimens determined by designators of neotypes and the author of the holotype were examined. Therefore, in each description there are separate sections for neotype or holotype and distribution, with ranges summarized from published records. Material personally examined for the three Palaearctic species is listed in appendix 2 along with material examined for previously described Nearctic species. Range maps are not provided for Palaearctic species.

Labels on holotypes of new species are reported with slashes separating contents of different lines of labels. Other labels have not been so treated. The contents of these labels have been reported exactly as they read, without corrections of punctation, such as missing periods after abbreviations. Locality data have been altered in only two ways. For some series of specimens from the same locality collected by one person on various days, or by several persons on the same day or days, the data are summarized and the locality is given only once. This method of summarization is only used where the information is clear. For popular localities collected by numerous individuals at numerous times (*S. neomexicanus* Muesebeck taken from Sagehen, California for example. Appendix 2, pp. 180-181), the labels are not summarized. On some labels, data given are insufficient for convenient identification of localities. For such labels, additional information which does not appear on the labels is included in square brackets.

In descriptions and various discussions, characters states are referred to as belonging to certain species or species groups. It is here acknowledged that these states actually belong to *individuals* of these taxa, but are ascribed to the entire taxon to avoid numerous repetitions of

the words 'specimens of', 'adults of', 'larvae of', *etc.*

2.2.6 Criteria for Species Discrimination

The application of biological (Mayr 1963) or evolutionary (Simpson 1951, Wiley 1978) species concepts to a systematic study of a collection of preserved material presents great practical difficulty. The major portion of such concepts include such dynamic phenomena as reproductive isolation and evolutionary change through time, neither of which are represented conclusively in preserved specimens. Therefore, the emphasis in this study has been placed on two criteria, phenetic and distributional characters, that give evidence of species status of populations.

Two populations that retain phenetic distinctiveness in spite of overlap of geographic range are considered to be reproductively isolated from one another and are therefore assumed to be separate species. The degree of phenetic difference between such species is used as an estimate of species status in phenetically distinct populations that are geographically isolated.

2.2.7 Criteria for Discrimination of Species Groups

Species groups are distinguished by differences in evolutionary trends. The *S. falcatus*-group displays marked trends in the evolution of genitalia in both sexes (sect. 4), whereas the *S. lateralis*-group does not. Species of the *S. lateralis*-group are relatively similar to one another in habitus, displaying slight character evolution, whereas species of the *S. falcatus*-group are relatively more divergent from one another. Both species groups are believed to be monophyletic on the basis of several shared derived character states.

3. TAXONOMIC TREATMENT OF THE GENUS *Sathon*

3.1 Classification

The genus *Sathon* was erected by Mason (1981) for Nixon's (1965) *falcatus*-group of *Apanteles* Förster, part of Nixon's *A. vitripennis*-group and a North American species Nixon did not treat. When Mason (1981:78) erected *Sathon*, he expressed some doubt about the placement of the species taken from the *A. vitripennis*-group [*S. lateralis* Haliday and *S. eugeni* Papp (=*S. fausta* Nixon)], because of the absence of some derived character states shared by other species of *Sathon*. *S. lateralis* and *S. eugeni* share the retracted and glabrous lobe of the metanotum and the reduced median carina of the propodeum with other *Sathon* species, but lack the truncate paramere of the male and the variably developed, specialized shape of the posterodorsal margin of the female hypopygium.

Examination of several species of *Choeras* Ashmead, the genus most closely related to *Sathon*, has revealed that the synapotypies between the species taken from the *A. vitripennis*-group and other *Sathon* species are not very reliable. Some specimens of *Choeras* exhibit a partially retracted (although setose) metanotal lobe and a partially reduced median propodeal carina. Also, some specimens of *Sathon* exhibit a few setae on the metanotal lobe and others display an almost complete propodeal carina. However, *Choeras* is a large and inadequately understood genus. Without substantial revisionary work and analysis of character evolution and distribution in the genus, I cannot make a conclusion about the reliability of the metanotal and propodeal characters that define *Sathon*. I therefore retain *S. lateralis* and *S. eugeni* in *Sathon*.

Sathon is organized in two species groups, the *S. lateralis*-group which contains the two species above plus *S. papilionae* new species, and the *S. falcatus*-group which contains the rest

of the species in the genus. The *S. lateralis*-group is considered less apotypic than the *S. falcatus*-group because of the characters dicussed above (see also 'Evolutionary Trends'), with one exception. All species in the *S. lateralis*-group have the median carina reduced to a trace or lost completely, whereas species of the *S. falcatus*-group have retained a trace or have the median carina partially developed.

The name for the *S. falcatus*-group has been retained from Nixon (1965), despite the inclusion of the type species of *Sathon*, *S. neomexicanus* Muesebeck. Nixon's *A. falcatus*-group contains the same previously described species as my *S. falcatus*-group. His *A. falcatus*-group is characterized by the truncate male paramere, agreeing with my characterization.

Dissection of female genitalia revealed that some species, described and undescribed, that had been placed by Mason in *Sathon* do not belong in the genus. Dissections of females of *Lathrapanteles papaipemae* Muesebeck and three previously undescribed species revealed genitalia similar to those of the Cotesiini, whose species parasitize macrolepidopterans and are more apotypic than species of the Microgastrini (Williams 1985). *L. papaipemae* females have a robust T9 of the metasoma, anterior apodeme of T9, and second valvifer. Moreover,the third valvula is attached near the base of the second valvifer. Examination of the last instar larval integument of *L. papaipemae* showed features common to cotesiine larvae. In all, *L. papaipemae* and the three previously undescribed species are apotypic in 10 of 14 characters used by Mason (1981, Table 2) to characterize the macrolepidopteran-parasitizing Microgastrinae, whereas *Sathon* species are apotypic in only three (or in apotypic *Sathon* species, five. See Williams 1985). As part of this study, but in a separate paper (Williams 1985), a new genus was erected for *L. papaipemae* and the three undescribed species were described. Therefore, although they were originally treated as *Sathon* species when this study was undertaken, they receive no further discussion.

3.2 Description of *Sathon*

Sathon Mason 1981.

Microgaster; Haliday 1834: 242, 248 (in part). --Nees von Esenbeck 1834: 175 (in part). --Curtis 1837: 116, 117 (in part).

Apanteles; Marshall 1872: 104, 105 (in part). --Muesebeck 1920 (1921): 526, 529 (in part). --Muesebeck 1922: 16 (in part). --Gautier & Cleu 1927: 85 (in part). --Wilkinson 1937: 463 (in part). --Fahringer 1938: 9 (in part). --Hincks 1944: 20 (in part). --Wilkinson 1945: 121, 133 (in part). --Strickland 1946: 37 (in part). --Muesebeck and Walkley 1951: 125, 131 (in part). --Muesebeck 1958: 29 (in part). --Nixon 1965: 186 (in part). --Muesebeck 1967: 41, 43 (in part). --Shenefelt 1972: 551 (in part). --Papp 1972: 336 (in part). --Nixon 1973: 177, 186 (in part). --Papp 1983: 260 (in part).

Sathon Mason 1981: 78 (description). Type species *Apanteles neomexicanus* Muesebeck 1920 (1921). Original designation. --Williams 1985: 1962 (some species removed from *Sathon*) .

Diagnosis.- Adults of *Sathon* are differentiated from those of other genera of Microgastrinae by the following combination of character states: metanotum with sublateral lobes slight asetose convexities (some specimens of *S. eugeni* with few setae); propodeum with median carina absent at base or almost completely, but marked by at least a trace of rugosity; T1 of metasoma somewhat narrow, length approximately three times apical width or more; T2 subtriangular; hypopygium evenly sclerotized and without striae midventrally; ovipositor and

third valvula at least 0.5 times as long as hind tibia; third valvula partly to completely polished and shining, attached near apex of second valvifer; T9 height 2.0 or more times width; second valvifer slender, narrow at apex.

Description.

Female. *Color*. Head and mesosoma rufopiceous to black; metasoma black, with white or fulvous spot on anteriormost lateroterga, to almost completely fulvous except for rufopiceous terga at base and apex of metasoma; antenna brown or black, some species with scape fulvous; legs fulvous or rufofulvous, some species with piceous coxae or areas on femora or tibiae and tarsi; third valvula fulvous to piceous.

Head. Width 1.54 - 2.08 times length. Occiput narrowly and shallowly (fig. 1) or broadly and somewhat deeply (fig. 134) indented medially, but not distinct from vertex and genae. Clypeus 2.50 - 3.90 (fig. 2) times wide as high; dorsal margin obscure or distinct and ventral margin with or without reflexed rim. Face with median carina on dorsal 0.2 to 0.4. Malar space sculptured or smooth posteriorly, furrow from ventral margin of eye to anterior mandibular articulation present or absent. POL/OOL = 0.62 - 1.78; POL/LOL = 1.75 - 3.25; LOD/AOD = 0.89 - 1.43; LOL/AOD = 0.47 - 1.33 (fig. 1). Penultimate flagellomere width 0.50 - 1.00 times length (fig. 5). Oral plate markedly narrowed ventrally or not, with or without median lines or area of pigmentation, dorsal margin concave to convex (figs. 17, 32, 35, 77, 90, 103, 117, 131).

Mesosoma. Pronotum (figs. 8, 23, 38, 45, 61, 68, 81, 94, 108, 122) with dorsal groove straight or decurved and smooth to moderately sculptured; ventral groove faintly sculptured to markedly foveolate and rugose anteriorly; ventral margin sinuate; ventral polished band width at posteroventral angle three to more than five times width at collar, smooth or striate posteriorly, band bottle shaped or not, with sinuation of ventral margin and ventral groove

matched or not; pronotal disc with slight to distinct punctures on dorsal 0.33 or more of surface; discal pit slight to distinct. Propleuron striate or punctate posterolaterally. Mesoscutum with punctures obscure to moderately developed on posterior part; setae posteriorly directed on anterior half, but posteromedially directed on posterior half in some species, line of setal convergence present or absent. Prescutellar furrow (figs. 9, 24, 39, 46, 62, 69, 82, 95, 109, 123) straight or arcuate, with anterior margin obscure or distinct; foveolation faint, especially medially, or distinct throughout. Scutellum (figs. 10, 25, 40, 47, 63, 70, 83, 96, 110, 124) with lunule as wide as or narrower than costate area, with dorsal margin evenly convex or irregular; costate area with costae absent medially or present throughout, in some species irregular carinae extended between costae; dorsal margin of costate area smooth or with sculpture on median polished part of scutellum; posterior margin of scutellum with slight or distinct median lobe. Metanotum (figs. 12, 27, 42, 49, 55, 72, 85, 98, 112, 126) with lateral convexity or moderate sublateral lobe, lobe without setae (except in some specimens of *S. eugeni* Papp); posterior margin simple or with foveolate rim; medial pit slightly sculptured or smooth, with sides straight, irregular or anteriorly divergent; lateral pits nearly smooth to markedly sculptured, narrower or wider than part of metanotum anterior to pit, with or without a well delimited anterior margin. Metapleuron (figs. 11, 26, 41, 48, 71, 84, 97, 111, 125) with median groove obsolete or distinct and sculptured; sculpture on posterior portion of metapleuron slight and limited to extreme posterior end or marked and covering most of surface; posteroventral carina angulate and widened or round and narrow near hind coxa. Propodeum (figs. 12, 27, 42, 49, 55, 72, 85, 98, 112, 126) smooth and with distinct punctures to areolate rugose, with or without lateroapical tubercles; median carina extended over most of propodeal length but absent at extreme base, or absent except as trace of rugosity; spiracle round to elongate oval, separated from pleural carina by 0.5 or more of its least diameter, in some species connected to pleural carina by carina or raised area; medioapical boss round, medially thickened, or triangular.

Tarsal claws longer or shorter than width of apical tarsomere. Penultimate fore tarsomere length 1.00 - 1.83 times width. Inner midtibial spur slightly to nearly twice as long as outer and 0.75 to as long as middle basitarsus. Inner hindtibial spur subequal to or slightly longer than outer, less or slightly more than 0.5 as long as hind basitarsus. Head width 0.88 - 1.53 hind coxa length; punctures on hind coxa absent, present in longitudial band or distinct on lateral surface (figs. 14, 29, 44, 52, 58, 74, 87, 100, 114, 128).

Fore wing (fig. 6) with stigma approximately 2.0 - 3.0 times long as wide; Rs base shorter or longer than thickness of SC+R and inserted basally or subbasally on parastigma; 2A present or absent; 2r length 0.57 - 1.83 1Rs length; 1Rs+M curved, nearly straight, or sinuate; 1Rs+M length 0.92 - 1.26 1M length; 1Cu1 length 0.74 - 1.39 m-cu length. Hind wing with Cu+cu-a evenly curved or sinuate; SC+R with bulb at extreme base that protrudes above upper plane of wing (figs. 54, 67), or only with slight convexity.

Metasoma. T1 (figs. 13, 28, 43, 50, 56, 73, 86, 99, 113, 127) narrow, at least 3.0 times longer than wide at apex; smooth over most of surface to markedly rugose; apex narrower than base, with straight, curved, or slightly sinuate sides; apex slightly to extremely convex medially. T2 (figs. as for T1) subtriangular, with lateral margins straight, curved, slightly sinuate, or obscured by rugosity; rugose, some species with median smooth area; apical margin straight, curved, or sinuate. T3 smooth or sculptured at extreme base; setae evenly distributed except for small or moderately large mediobasal area; apex desclerotized and whitened or not. T4 to T7 desclerotized and whitened or not; setae limited to single apical row medially, or evenly distributed. Island oval to elongate oval, in one species keyhole-shaped, progressively more elongate toward metasoma apex. Hypopygium (figs. 18, 33, 36, 53, 64, 78, 91, 104, 118, 132) with setae absent midventrally along length or only at midlength; apex entire or emarginate; median ventral area evenly sclerotized and without striae; posterodorsal margin straight, angulate, or sinuate, with or without subapical lobe. T9 (figs. 16, 31, 34, 76, 89, 102, 116, 130) approximately 2.0 to 3.0 times high as wide; anterior apodeme slightly developed. Second

valvifer (figs. as for T9) slender, narrowed apically; short and not extended into dorsal 0.5 of T9, or long and extended nearly to dorsal margin of T9; apex rounded, irregular, immarginate, or with differentiated head or apodeme. Third valvula (figs 16, 31, 34, 53, 64, 76, 89, 102, 116, 130) 0.47 - 1.28 times length of hind tibia; partly to completely polished; attached to second valvifer near valvifer's apex; straight or decurved, ventral margin convex or concave and extensively desclerotized or evenly sclerotized; setae on apical 0.66 or more, evenly distributed or concentrated on ventral half, in one species apical setae bent-tipped; apex with narrow and triangular or broad desclerotized area. Ovipositor decurved, evenly (figs. 16, 31, 34, 53, 64, 89, 102) or markedly more near apex than near base (figs. 76, 116, 130); approximately 1.0 to 2.0 times as long as hind tibia, with or without subapical constriction; basal bulb slightly (figs. 16, 31, 35) to markedly (figs. 76, 89, 102, 116, 130) set off from shaft.

Male. Similar to female, except: in most species color tones of most body parts darker than in female; antennae elongate relative to female, penultimate flagellomere width at most 0.5 times length; propodeum with sculpture less developed than female in most species (figs. 15, 59, 75, 88, 101, 115, 129); T1 and T2 of metasoma (figs. as for propodeum except *S. aggeris* where it is fig. 60) slender relative to female, in some species with less developed sculpture; paramere rounded or truncate and narrowed or markedly widened at apex (figs. 21, 22, 65, 66, 79, 80, 92, 93, 106, 107, 120, 121, 135, 136), sides curved or nearly straight; aedeagus ovoid or triangular in cross section and slightly or distinctly knobbed at apex; digitus short or elongate (figs. as for paramere); basal ring medially sclerotized or desclerotized, with or without median carinae (figs. as for paramere).

Cocoon. White, solitary or in oblong mass.

Larva (figs. 19, 37, 119, 133). Solitary or gregarious. Hypostoma with one to three mandibular processes and small or marked spur; mandible blade straight or curved and with row of straight

and regular or irregular teeth on apical 0.50 to 0.66; silk press with thin or thick integument, internal details not or extensively visible in cleared specimens; labial sclerite wider than high or higher than wide.

Hosts.- Hosts are known only for *S. lateralis*, *S. papilionae*, *S. eugeni*, *S. falcatus* and *S. neomexicanus*. These species have been reared from lepidopterous larvae of the following families: Geometridae, Glyphipterygidae, Gracillariidae, Hepialidae, Lymantriidae, Noctuidae, Olethreutidae, Papilionidae, Pterophoridae, Pyralidae, Sesiidae and Yponomeutidae.

Distribution.- The range of this genus extends throughout the Holarctic region, and also into the Neotropical (as far south as Colombia) and Oriental (Java) regions.

Chorological and Phylogenetic Affinities.- *Sathon* species are sympatric with *Choeras* Ashmead species, as the latter genus is cosmopolitan. The significance of this is unknown as the exact relationship between the genera is uncertain.

Sathon is apparently closely related to *Choeras*, from which it differs only in the structure of the metanotum and hypopygium. I have examined several undescribed species of *Choeras* that are very similar to *S. lateralis*-group species. One such species is included in the outgroup used for character polarization (see 4.1). It is not currently known if the diverse genus *Choeras* is delimited by any synapotypies relative to *Sathon* or any of the more derived genera in the tribe. Given the similarity of some apotypic *Choeras* species to *Sathon*, it is possible that *Choeras* is paraphyletic to *Sathon*. It is also possible that the *S. falcatus*- and *lateralis*-groups are independently derived from *Choeras* stock. This possibility is suggested by the retention of submedial metanotal setae in some specimens of *S. eugeni* Papp, which reduces the value of the primary diagnostic feature of *Sathon* species relative to other members of the tribe. Unfortunately, the majority of *Choeras* species are unknown, and the genus is very large. Description of many of the more apotypic species and careful examination of character

evolution in this genus must be made before any definite change in the taxonomic status of *Sathon* can occur.

3.3 Keys to species of *Sathon*

3.3.1 Key to Females

1. T2 of metasoma with lateral margins delimited by anteriorly curved grooves (figs. 13, 28, 43). Hypopygium with evenly curved posterodorsal margin (fig. 18). . ..... (*S. lateralis*-group)..2

1'. T2 of metasoma with lateral margins obscured by rugosity (fig. 73) or delimited by nearly straight grooves (fig. 127). Hypopygium with angulate (fig. 78) or sinuate (fig. 132) posterodorsal margin (weakly sinuate in *S. laevidorsum* new species). .....(*S. falcatus*-group)..4

2(1). Hind coxa mostly fulvous and with punctures obscure (fig. 44).....
.....*S. eugeni* Papp, p. 32

2'. Hind coxa mostly piceous and with punctures distinct (fig. 14).. 3

3(2). Propodeum nearly smooth apically (fig. 27). Hind leg darkened apically but without distinct piceous areas. ..... *S. papilionae* new species, p. 29

3'. Propodeum sculptured apically (fig. 12). Hind leg with distinct piceous area on apex of tibia and usually on apex of femur.. .....*S. lateralis* Haliday, p. 26

4(1). Posterior margin of metanotum with rim conspicuous in dorsal aspect (figs. 49, 55). Inner midtibial spur nearly as long as middle basitarsus.....5

4'. Posterior margin of metanotum with rim absent or inconspicuous in dorsal aspect (fig. 72). Inner midtibial spur at most 0.75 of middle basitarsus length.. ..
.....6

5(4). Propodeum and T1 of metasoma markedly rugose (figs. 55, 56). T1 medially protuberant (fig. 57). Metasoma with white lateral band. .... *S. aggeris* new species, p. 38

5'. Propodeum and T1 of metasoma nearly smooth except for a few punctures (figs. 49, 50). T1 slightly convex (fig. 51). Metasoma mostly piceous with anterolateral fulvous area. . ..... *S. laevidorsum* new species, p. 35

6(4). Propodeum with raised lateroapical carinae and rugosity (fig. 72). Hypopygium with posterodorsal margin angulate (fig. 78)..... 7

6'. Propodeum nearly smooth or with low wrinkles (fig. 126) Hypopygium with posterodorsal margin sinuate (fig. 132). 8

7(6). Color predominantly piceous except for legs and anteriormost lateroterga of metasoma. Third valvula piceous and with all setae straight (fig. 76). Ovipositor evenly decurved and with marked subapical constriction (fig. 76).. .... *S. masoni* new species, p. 42

7'. Color predominantly rufopiceous with extensively fulvous metasoma. Third valvula fulvous and with apical setae bent-tipped (fig. 89). Ovipositor sharply decurved at apical 0.33 and without subapical constriction or with very slight one (fig. 89). ..... *S. cinctiformis* Viereck, p. 47

8(6). Ovipositor (including part hidden by hypopygium) slightly longer than hind tibia, evenly but markedly decurved over most of length (fig. 102).. .... *S. circumflexus* new species, p. 51

8'. Ovipositor (including part hidden by hypopygium) approximately twice as long as hind tibia, more decurved apically than basally (fig. 130)..... 9

9(8). Occiput narrowly and shallowly indented medially (fig. 1). 3Rs of fore wing slightly sinuate, decurved near wing apex. T1 of metasoma with wide medioapical smooth area (fig. 113). Hypopygium sclerotized and entire apically (fig. 118). ... . *S. neomexicanus* Muesebeck, p. 55

9'. Occiput concave medially, head arc-shaped (fig. 134). 3Rs of fore wing straight, usually not decurved near wing apex. T1 of metasoma with narrow or no medioapical smooth area (fig. 127). Hypopygium slightly desclerotized and emarginate apically (fig. 132).. ..... *S. falcatus* Nees, p. 60

3.3.2 Key to Known Males

1. T1 of metasoma evenly narrowed apically, with sides straight, length approximately 4 times apical width and sculpture absent except in lateroapical areas (fig. 15). T2 with lateral margins delimited by anteriorly curved grooves. Aedeagus ovoid in cross section at midlength. Paramere rounded at apex (fig. 22, *S. lateralis*-group).. .....*S. lateralis* Haliday, p. 26

1'. T1 of metasoma parallel sided or more gradually narrowed basally than apically, with sides sinuate or curved, length less than 4 times apical width (approximately 4 in *S. circumflexus* n. sp.), and sculpture present over most of surface (figs. 60, 75, 88, 101, 115, 129). T2 with lateral margins obscured by rugosity or delimited by nearly straight grooves. Aedeagus triangular in cross section at midlength. Paramere truncate at apex (figs. 66, 136, *S. falcatus*-group).. 2

2(1). Propodeum with raised carinae and rugosity lateroapically (fig. 75). T2 of metasoma with lateral margins obscured by rugosity (fig. 75)..... 3

2'. Propodeum smooth or with low rugosity lateroapically (fig. 101). T2 of metasoma with lateral margins delimited by grooves (fig. 101)..... 4

3(2). Head and mesosoma rufopiceous, metasoma predominantly fulvous. Hind coxa fulvous. Posterior part of metapleuron extensively punctate and sculptured, with carina extended from posterior rim (fig. 71). . ..... *S. cinctiformis* Viereck, p. 47

3'. Body predominantly piceous. Hind coxa piceous basally. Posterior part of metapleuron with few punctures, sculpture limited to area near posterior rim,

and without carina (fig. 84).. ..... *S. masoni* new species, p. 42

4(2). Posterior margin of metanotum with foveolate rim (fig. 59). T2 of metasoma with lateral margins delimited by concave grooves (fig. 60). Legs with longitudinal bands of piceous coloration.. .....*S. aggeris* new species, p. 38

4'. Posterior margin of metanotum without rim (fig. 101). T2 of metasoma with lateral margins delimited by approximately straight grooves (fig. 101). Legs fulvous, darkened apically..... 5

5(4). T1 of metasoma slender, approximately as wide at apex as medioapical boss of propodeum (fig. 101). T2 longer than wide, with posterior margin slightly sinuate (fig. 101). Paramere slightly longer than T1. . ... *S. circumflexus* new species, p. 51

5'. T1 of metasoma wider at apex than medioapical boss of propodeum (fig. 129). T2 wider than long and with posterior margin markedly sinuate (fig. 129). Paramere longer than T1+T2. 6

6(5). Fore and middle coxae mostly piceous. Hind coxa entirely piceous, with distinct punctures on most of lateral surface (fig. 128). Parameres in contact midventrally in a broad band at base, apical truncation slightly oblique (figs. 135, 136).. ..... *S. falcatus* Nees, p. 60

6'. Fore and middle coxae mostly or entirely fulvous. Hind coxa fulvous at least at extreme apex, with punctures obscure over most of lateral surface except for a midlateral band (fig. 114). Parameres in contact midventrally in a narrow band at base, apical truncation markedly oblique (figs. 120, 121).. .... *S. neomexicanus* Muesebeck, p. 55

3.4 The *S. lateralis-group*

Adults of the *S. lateralis*-group are differentiated from those of the *S. falcatus*-group by the following combination of character states: costate area of scutellum with costae faint or absent over wide medial area (fig. 10); propodeum with median carina short or absent (fig. 12); T2 of metasoma with lateral margins delimited by anteriorly curved grooves and posterior margin nearly straight (fig. 13); T3 with setae evenly distributed except for small mediobasal area; apical unsclerotized and unpigmented area of T6 and T7 more pronounced at medially than laterally, both terga appearing somewhat emarginate in specimens with fully expanded metasomas (fig. 20); female with posterodorsal margin of hypopygium evenly curved and with third valvula straight (figs 16, 18); male (where known) with paramere rounded apically and aedeagus ovoid in cross section (fig. 22).

3.4.1 *Sathon lateralis* Haliday 1834.

Microgaster lateralis Haliday 1834: 248; type lost, Neotype designated by Wilkinson 1945: 121.

Apanteles lateralis; Marshall 1872: 105.

Sathon lateralis; Mason 1981: 80.

Neotype.- Male, Bignell Collection, Plymouth Museum. Reg. No. 2076. Designated by Wilkinson (1945: 123).

Diagnosis.-

Female. *Color*. Head and mesosoma piceous; metasoma piceous, with anterolateral fulvous area on anteriormost lateroterga; antenna piceous; fore and middle legs fulvous, hind

leg fulvous with coxa, dorsodistal area of femur, distal end of tibia and all tarsomeres infuscate; third valvula dark rufopiceous.

Head. Oral plate evenly pigmented, with dorsal margin flat but medially desclerotized (fig. 17).

Mesosoma. Pronotum (fig. 8) with dorsal groove smooth or slightly sculptured; ventral groove with slight foveolations. Mesoscutum with punctures obscure on most of surface. Scutellum (fig. 10) with costae moderately distinct, or faint medially and absent anteriorly; anterior groove deep, crossed by very faint to distinct costae; dorsal groove shallow and very narrow anteriorly; posterior margin of scutellum with marked median lobe. Metanotum with moderate convexity or marked sublateral lobe on anterior margin (fig. 12). Propodeum punctate basally, rugose near medioapical boss and in some specimens lateroapically (fig. 12).

Inner midtibial spur longer than outer and nearly as long as middle basitarsus. Hind coxa with punctures distinct (fig. 14).

Metasoma. T1 (fig. 13) smooth mediobasally, rugosopunctate elsewhere; apex narrower than base, with sides straight or slightly sinuate near apex. T2 (fig. 13) with lateral margins slightly to moderately sinuate; rugose, but with sculpture faint or absent medially in some specimens: apical margin slightly convex or slightly sinuate. Hypopygium (fig. 18) with setae absent midventrally; apex entire. T9 approximately 2.0 times higher than wide (fig. 16). Second valvifer projected into upper 0.5 of T9, apex immarginate (fig. 16). Third valvula (fig. 16) with setae evenly distributed; apex with broad desclerotized area. Ovipositor (fig. 16) evenly slightly decurved; approximately as long as hind tibia, without subapical constriction; basal bulb not markedly set off from shaft.

Male. Similar to female, except: some specimens with antennae rufopiceous; medioapical boss triangular in some specimens; T2 with sculpture effaced or lateral margins obscured by rugosity

(fig. 15); paramere irregularly rounded and narrowed at apex, length much less than 0.33 of metasoma (fig. 22); aedeagus triangular in cross section at midlength, oval elsewhere, apex slightly knobbed (fig. 22); digitus short, apex scarcely longer than broad (fig. 22); basal ring slightly sclerotized midapically, without median carinae (fig. 21).

Cocoon. Elongate oval, round in cross section, without flattened or slightly translucent sides.

Larva. (fig. 19) Gregarious. Hypostoma with one small mandibular process and slight hypostomal spur; mandible blade curved at apex, with single row of straight, regular teeth on apical 0.5; silk press apparently with thin integument, only external details visible; labial sclerite approximately wide as high.

Hosts.- *S. lateralis* has been reared from larvae of the following species of Lepidoptera: *Tephroclystia assimilata* Dbld., *Liparis auriflua* L., *Porthesia chrysorrhoea* L., *Anthophila fabriciana* L., *Yponomeuta padella* L., *Elachista taeniatella* Staint, *Galleria mellonella* L., *Priobium carpini* Hbst. and *Gracillaria syringella* F. (see Shenefelt 1972 for citations of rearing records).

Phylogenetic Affinities.- *S. lateralis* is the sister species to *S. eugeni* + *S. papilionae* .

Distribution.- Western part of the Palaearctic Region. Published records are from Finland to Hungary, and from England to the U.S.S.R.

Chorological Affinities.- The range of this species overlaps with both *S. falcatus* and *S. eugeni*. Specimens of this species have been collected at localities where those of both other species have been found. Apparently sympatric with *S. eugeni*, a member of the sister group of *S. lateralis*.

3.4.2 *Sathon papilionae* new species

Holotype.- Female, Papilio zelicaon / Clayoquot / B.C. / No. 61-1491-0A2 / Date 20-VIII-61 / F.I.S. 1961 (CNC).

Derivation of Specific Epithet.- Latin, masculine, referring to the host from which this species was reared.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: propodeum smooth or with few wrinkles apically; hind coxa piceous on basal 0.75 and with marked punctation; T1 of metasoma evenly narrowed apically and with sculpture limited to lateroapical areas; T2 of metasoma with lateral margins delimited by sinuate grooves; hypopygium with posterodorsal margin evenly and gradually convex.

Description.-

Female. *Color*. Head and mesosoma piceous; metasoma with T1 and T2 piceous, apex and venter rufopiceous and lateroterga fulvous; antennae brown; fore and middle legs fulvous, hind leg fulvous with coxa piceous on basal 0.75 and hind tibia rufopiceous at apex; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially. Clypeus with dorsal margin distinct, ventral margin with reflexed rim medially obscure. Face with median carina on dorsal 0.4. Malar space sculptured posteriorly except near eye; furrow from ventral margin of eye to anterior mandibular articulation complete. Oral plate evenly pigmented, with dorsal margin concave (fig. 32).

Mesosoma. Pronotum (fig. 23) with dorsal groove straight and deeply impressed, but smooth; ventral groove slightly foveolate, more foveolate anteriorly than posteriorly, area of junction with dorsal groove smooth; ventral margin slightly sinuate; width of ventral polished band at posteroventral angle approximately four times width at collar, smooth posteriorly, band not bottle shaped with sinuation of ventral margin and ventral groove not matched; pronotal disc with punctures on dorsal 0.5 - 0.75; discal pit obscure. Propleuron punctate posterolaterally. Mesoscutum with punctures obscure, relatively less so anteriorly than posteriorly; setae posteromedially directed near prescutellar furrow but posteriorly directed elsewhere, without line of setal convergence. Prescutellar furrow (fig. 24) straight medially, anterior margin delimited medially or not; cross carinae as high as scutellum or nearly so laterally, but carinae lower medially. Scutellum (fig. 25) with lunule narrower than costate area and with dorsal margin more convex medially than laterally; costate area with costae faint medially and anteriorly; anterior furrow wide, deep and smooth; dorsal groove shallow and narrow; dorsal margin of costate area with some surface irregularity on polished median part of scutellum; posterior margin of scutellum with distinct median lobe. Metanotum (fig. 27) laterally convex; posterior margin without rim; medial pit smooth, approximately parallel sided; lateral pits partly rugose and with smooth areas, wider than part of metanotum anterior to pit, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 26) with median groove smooth, obsolete near midpit; slight sculpture on posterior 0.3 of posterior portion of metapleuron, but distinct punctures anterior to this; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 27) with scattered shallow punctures basally, smooth or with slight rugose sculpture apically; spiracle oval, separated from pleural carina by less than its own least diameter; medioapical boss round, slightly thickened medially.

Tarsal claws shorter than width of apical tarsomere. Inner midtibial spur longer than outer and nearly as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures deep and distinct

on most of surface (fig. 29).

Fore wing with Rs base as long or longer than thickness of SC+R and inserted subbasally on parastigma; 2A absent; 2+3Rs slightly curved or straight, not decurved apically; 1Rs+M nearly straight. Hind wing with Cu+cu-a evenly curved or more curved near junction with M+Cu than near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 28) slightly to moderately rugosopunctate lateroapically; apex narrower than base, with sides straight and apically convergent; apex moderately convex. T2 (fig. 28) with lateral margins sinuate; rugose laterally, polished medially; apical margin slightly sinuate. T3 with limited sculpture near furrow delimiting anterior margin; setae sparse; apex not desclerotized or whitened. T4 to T7 narrowly desclerotized, not whitened; setae scattered across each tergum, but sparse on T4. Islands elongate oval. Hypopygium (fig. 33) with setae absent midventrally at midlength; apex entire medioventrally. T9 approximately 1.8 times higher than wide (fig. 31). Second valvifer (fig. 31) extended into dorsal half of T9, apex rounded and anteriorly deflected. Third valvula length 0.60 - 0.68 hind tibia length; setae on apical 0.75, concentrated apically but evenly distributed dorsoventrally; apex with triangular desclerotized area. Ovipositor (fig. 31) evenly and gradually decurved; approximately as long as hind tibia, with very slight subapical constriction; basal bulb not markedly set off from shaft.

Male. Unknown.

Cocoon, Larva. Unknown.

Hosts.- Reared from *Papilio zelicaon* Lucas by the Forest Insect Survey.

Phylogenetic Affinities.- *S. papilionae* is the sister species of *S. eugeni*.

Distribution.- Known only from the localities listed for type material.

Chorological Affinities.- The range of this species apparently overlaps with those of *S. neomexicanus*, *S. circumflexus* and *S. masoni*, but *S. papilionae* is the only known Nearctic member of the *S. lateralis*-group. It is apparently allopatric with its sister species, *S. eugeni*.

Paratypes.- Two females, Cold Bay 163° W. Alaska 21-VIII 1952, W.R. Mason (CNC).

3.4.3 *Sathon eugeni* Papp 1972.

Apanteles eugeni Papp 1972: 336.

Apanteles magnicoxis Jakimavičius 1972: 306-308. Synonymy by Papp 1983: 260.

Apanteles fausta Nixon 1973: 177. Synonymy by Papp 1983: 260.

Sathon fausta; Mason 1981: 80.

Holotype.- Female, Hungarian Natural History Museum, Reg. No.2001.

Diagnosis.-

Female. *Color*. Head and mesosoma piceous; metasoma piceous except for large fulvous area extended over most lateroterga and fulvous on apex of hypopygium, or entirely fulvous except for terga which are rufopiceous to piceous; antenna light brown; fore and middle legs fulvous, hind leg with coxa piceous basally or entirely fulvous and apex of tibia and all tarsomeres darkened, rest of leg fulvous; third valvula rufopiceous to piceous.

Head. Clypeus with dorsal margin indistinct or completely effaced. Oral plate evenly pigmented, with dorsal margin flat but medially desclerotized (fig. 35).

Mesosoma. Pronotum with dorsal groove smooth or very slightly sculptured; ventral groove with slight foveolations (fig. 38). Mesoscutum with punctures obscure or absent over at least posterior 0.5. Scutellum (fig. 40) with costae faint medially and anteriorly, or absent except posteriorly and in dorsal groove; anterior groove deep, smooth, crossed by indistinct costae or costae absent; dorsal groove very narrow and shallow anteriorly; posterior margin of scutellum with marked median lobe. Metanotum with setae on sublateral lobe in some specimens (fig. 42). Propodeum with slightly to moderately developed punctures basally, rugose near medioapical boss (fig. 42).

Inner midtibial spur markedly longer than outer and nearly as long as middle basitarsus. Hind coxa with punctures faint on lateral surface (fig. 44).

Metasoma. T1 (fig. 43) smooth basally and in some specimens medially, punctate or rugosopunctate elsewhere; apex narrower than base, with sides straight. T2 (fig. 43) with lateral margins sinuate, but partially obscured by rugosity in some specimens; rugose, but with sculpture faint medially in some specimens; apical margin sligtly concave or nearly straight. T3 to T7 with apex desclerotized and slightly whitened. Hypopygium (fig. 36) with setae absent midventrally; apex immarginate. T9 approximately 2.25 times higher than wide (fig. 34). Second valvifer projected into upper 0.5 of T9, apex rounded and anteriorly deflected. Third valvula (fig. 34) with setae evenly distributed; apex with broad desclerotized area. Ovipositor (fig. 34) slightly decurved; approximately as long as hind tibia, without subapical constriction; basal bulb not markedly set off from shaft.

Male. Unknown.

Cocoon. Elongate oval, round in cross section, without flattened or slightly translucent sides;

with a thick strap of silk joined to cocoon by a thinner web.

Larva. (fig. 37) Solitary. Hypostoma with one large mandibular process and marked hypostomal spur; mandible blade curved at spex, with single row of straight, regular teeth on apical 0.5; silk press apparently with thin integument, only external details visible; labial sclerite wider than high.

Hosts.- *S. eugeni* has been reared from larvae of *Anthophila fabriciana* (L.) (Nixon 1973).

Phylogenetic Affinities.- *S. eugeni* is the sister species of *S. papilionae* new species.

Distribution.- Western part of the Palaearctic Region. Published records are from Sweden to Austria, and from England to the western U.S.S.R.

Chorological Affinities.- The range of this species overlaps with both other Palaearctic *Sathon* species. *S. eugeni* has been collected at sites where both *S. falcatus* and *S. lateralis* have been found, but is apparently allopatric with its Nearctic sister species, *S. papilionae*.

3.5 The *S. falcatus*-group

Adults of the *S. falcatus*-group are differentiated from those of the *S. lateralis*-group by the following combination of character states: costate area of scutellum with costae complete medially, although variably developed (figs. 47, 63, 70, 83, 96, 110, 124); propodeum in most specimens with at least trace of median carina at apex or with median carina distinct (figs. 49, 55, 72, 85, 98, 112, 126); T2 of metasoma with lateral margins obscured by rugosity or delimited by straight or slightly curved grooves, posterior margin nearly straight to markedly sinuate (figs. 50, 56, 73, 86, 99, 113, 127); T3 with setae absent in moderately sized mediobasal

area; T6 and T7 uniformly sclerotized and pigmented across width, not emarginate; females with posterodorsal margin of hypopygium angulate (fig. 78) and/or sinuate (fig. 132) and third valvula decurved in most species (figs. 53, 64, 76, 89, 102, 116, 130); male (where known) with paramere truncate at apex and aedeagus triangular in cross section over part or all of length (figs. 66, 80, 93, 107, 122, 136).

3.5.1 *Sathon laevidorsum* new species

Holotype.- Female, N. Cortez Pass, Mex., 10,000' 8-11-54. R.R. Dreisbach (CNC).

Derivation of Specific Epithet.- Latin, masculine, from 'laevis' meaning smooth and polished and 'dorsum'. It refers to the smoothness and general lack of sculpture, with the mesoscutal punctures obscure, the propodeum and T1 of the metasoma with little sculpture other than punctures and T2 of the metasoma medially smooth.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the following combination of characters: propodeum and metasomal T1 polished, with sculpture other than punctures only at apex; metanotum with posterior margin rimulose laterally; base of SC+R of hind wing with inflated bulb that protrudes above upper plane of hind wing.

Description.-

Female. *Color*. Head and mesosoma black; metasoma black with anterolateral fulvous spot; antennal scape piceous, slightly darker than flagellum; fore and middle legs fulvous with external surfaces of tibiae infuscate, hind leg with external surface and apex of tibiae and entire tarsi infuscate; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially. Clypeus with dorsal margin obscure and ventral margin without reflexed rim. Face with median carina on upper 0.2. Malar space smooth near eye, but sculptured near mandibular articulation; furrow from ventral margin of eye to anterior mandibular articulation obscure.

Mesosoma. Pronotum (fig. 45) with dorsal groove indistinct, slightly arcuate and without foveolation; ventral groove with foveolation indistinct and without rugosity anteriorly; ventral margin moderately sinuate; width of ventral polished band at posteroventral angle greater than five times width at collar, smooth posteriorly, band not bottle shaped, with sinuation of ventral margin and ventral groove not matched; pronotal disc with few slight punctures over most of surface; discal pit moderately deep and distinct. Propleuron punctate posterolaterally. Mesoscutum with punctures obscure posteriorly, slightly less so anteriorly; setae posteriorly directed anteriorly and laterally, posteromedially directed medially and posteriorly, with line of setal convergence. Prescutellar furrow (fig. 46) straight medially, shallow, with anterior margin distinct; cross carinae as high as scutellum laterally, faint medially. Scutellum (fig. 47) with lunule as wide as costate area and with dorsal margin evenly convex; costate area without costae medially; anterior groove crossed by several costae; dorsal groove narrow; dorsal margin of costate area smooth; posterior margin of scutellum with indistinct median lobe. Metanotum (fig. 49) laterally convex; posterior margin with differentiated, granulate rim laterally but not medially; medial pit sculptured, with irregular sides; lateral pits moderately sculptured and with some smooth areas, approximately as wide as part of metanotum anterior to pit, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 48) with median groove smooth and obscure near midpit; posterior portion of metapleuron with slight sculpture on posterior 0.33; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 49) punctate basally, with slight, irregular rugosity apically; without raised carinae; spiracles oval, nearly in contact with pleural carina; medioapical boss round.

Tarsal claw slender, longer than width of apical tarsomere. Inner midtibial spur nearly twice as long as outer and nearly as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures moderately distinct (fig. 52).

Fore wing with Rs base as long as thickness of SC+R and inserted basally on parastigma; 2A slight bulge on margin of 1A+2A; 2+3Rs very slightly sinuate, not decurved apically; 1Rs+M nearly straight. Hind wing with Cu+cu-a sinuate, markedly more curved near junction with M+Cu than at midlength and recurved near junction with 1A; SC+R at extreme base with bulb protruded above upper plane of wing (fig. 54).

Metasoma. T1 (fig. 50) smooth except for few punctures and slight lateral rugosity near apex; apex narrower than base, with sides sinuate; apex moderately convex. T2 (fig. 50) with lateral margins straight; rugose laterally and smooth medially; apical margin sinuate. T3 smooth; apex with slightly wider desclerotized band than following terga. T4 to T7 slightly desclerotized, not whitened apically; setae evenly scattered across terga. Islands elongate oval to slit-shaped. Hypopygium (fig. 53) with setae evenly distributed; apex entire medioventrally; posterodorsal margin with slight sinuation. Third valvula (fig. 53) straight, with ventral margin sclerotized and convex; setae on apical 0.66 but sparse, slightly more concentrated on ventral half; apex with desclerotized area triangular, longer than wide and with sclerotized band parallel to, but separate from, ventral margin. Ovipositor (fig. 53) slightly and evenly decurved; slightly longer than hind tibia and with very slight subapical constriction; basal bulb not markedly set off from shaft.

Male, Larva, Cocoon. Unknown.

Hosts.- Unknown.

Phylogenetic Affinities.- *S. laevidorsum* is the sister species of *S. aggeris* .

Distribution.- Known only from the type locality.

Chorological Affinities.- The range of this species does not overlap with any other *Sathon* species, and it is apparently allopatric with its sister species, *S. aggeris*. *S. laevidorsum* is the only known *Sathon* species from Central America.

Paratype.- Female, same data as holotype. Gold coated for S.E.M.

3.5.2 *Sathon aggeris* new species

Holotype.- Female, Ecuador 3900m / Quito-Baeza Rd. / Elfin For. / Mar. '79 W. Mason (CNC).

Derivation of Specific Epithet.- Latin, masculine, meaning heap or mound and referring to the unusually protuberant convexity of the first tergum of the metasoma in the female.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: first tergum of the metasoma very convex, especially in the female where it is developed into a tubercle; posterior margin of metanotum with a differentiated, foveolate rim; hind wing with SC+R with an enlarged tubercle protruding markedly above upper plane of wing.

Description.-

Female. *Color*. Head and mesosoma black with metallic blue highlights; metasoma black, with apical terga and hypopygium piceous, and lateral white stripe on lateroterga and dorsal margins of sternites which blends with black of terga and sternites and is narrowed posteriorly; antennae piceous; fore and middle legs fulvous and with apex of femora, external surfaces of tibiae and entire tarsi piceous, hind leg as other legs but also with trochanters and coxae black; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially. Clypeus with dorsal margin obscure and ventral margin without reflexed rim. Face with median carina on upper 0.2. Malar space with few scattered punctures, otherwise smooth; furrow from ventral margin of eye to anterior mandibular articulation absent except near eye.

Mesosoma. Pronotum (fig. 61) with dorsal groove straight and without foveolation; ventral groove with foveolation indistinct and without rugosity anteriorly; ventral margin moderately sinuate; width of ventral polished band at posteroventral angle more than five times width at collar, striate posteriorly, band not bottle shaped, sinuation of ventral margin and ventral grooved not matched; pronotal disc with few slight punctures on dorsal 0.33 of surface; discal pit moderately deep and distinct. Propleuron striate posterolaterally. Mesoscutum with punctures obscure posteriorly, slightly less so anteriorly; setae posteriorly directed on anterior half, posteromedially directed on posterior half, but without line of setal convergence. Prescutellar furrow (fig. 62) straight, with anterior margin merged with mesoscutum and obscure; cross carinae lower than scutellum and indistinct in some specimens. Scutellum (fig. 63) with lunule as wide as costate area and with dorsal margin evenly convex; costate area without costae medially; anterior furrow crossed by numerous distinct costae; dorsal groove extremely shallow; dorsal margin of costate area smooth; posterior margin of scutellum with slight median lobe. Metanotum (fig. 55) laterally convex; posterior margin with differentiated, foveolate rim; medial pit sculptured, straight sided; lateral pits robustly and entirely sculptured, wider than part of metanotum anterior to pit, with distinct anterior margin, part of metanotum

anterior to pit smooth. Metapleuron with median groove smooth and obsolete near midpit; slight sculpture on posterior 0.5 of posterior portion of metapleuron; posteroventral carina angulate and notably widened near hind coxa. Propodeum (fig. 55) areolate-rugose with lateroapical rugose tubercles; raised carinae absent; spiracle oval, nearly in contact with pleural carina; medioapical boss round.

Tarsal claws slender, longer than width of apical tarsomere. Inner midtibial spur nearly twice as long as outer and nearly as long as middle basitarsus. Inner hindtibial spur slightly longer than outer and more than 0.5 as long as hind basitarsus. hind coxa with punctures on hind coxa indistinct on lateral surface, distinct on dorsal surface (fig. 58).

Fore wing with Rs base nearly as long as thickness of SC+R and inserted subbasally on parastigma; 2A lightly pigmented trace visible almost to posterior wing margin; 2+3Rs slightly sinuate, slightly decurved apically; 1Rs+M sinuate. Hind wing with Cu+cu-a sinuate, markedly more curved near junction with M+Cu than at midlength and recurved near junction with 1A; SC+R at extreme base with bulb protruded above upper plane of wing (fig. 67).

Metasoma. T1 (fig. 56) rugose; apex wider than base, with sinuate sides; apex with very convex tubercle (fig 57). T2 (fig. 56) with lateral margins straight; rugose apically and longitudinally rugose basally; apical margin slightly sinuate. T3 sculptured at extreme base; apex desclerotized and whitened. T4 to T7 slightly desclerotized, not whitened apically; setae limited to apical half of each tergum, in form of single row medially. Island oval on laterotergum 3, progressively elongate posteriorly to slit-shaped on laterotergum 6. Hypopygium (fig. 64) with setae absent midventrally at midlength; apex entire medioventrally; posterodorsal margin sinuate and with slight lobe. Third valvula (fig. 64) straight, ventral margin extensively desclerotized and convex; setae on apical 0.66, concentrated on ventral half; apex with narrow, acute desclerotized area. Ovipositor (fig. 64) nearly straight; approximately as long as hind tibia; without subapical constriction; basal bulb not markedly set off from shaft.

Male. Similar to female, except: maxilla and labium brown; coxa piceous; tibiae, tarsi and entire hind leg rufopiceous except for piceous internal and external surfaces of femora and external surfaces of rest of leg; clypeus 2.0 as wide as high in some specimens; face with median carina obscure; eye with posterior margin convex; pronotum with few faint foveolations in dorsal groove; ventral polished band with few faint striae in most specimens; prescutellar furrow with cross carinae low but not faint; scutellar costate area with costae complete, both dorsal and anterior grooves slightly impressed; metanotum (fig. 59) with medial pit widened anteriorly and lateral pits without distinct anterior margin and extended nearly to anterior margin of metanotum; propodeum (fig. 59) without tubercles, rugosity low and with some smooth areas basally and lateroapically in some specimens; fore wing with 2A faint bulge on 1A+2A, 1Rs+M evenly curved; hind wing with 2A evenly curved; T1 of metasoma (figs. 59, 60) narrowed apically, areolate rugose to rugose and markedly convex but without medioapical tubercle; T2 of metasoma (fig. 60) with lateral grooves indistinct in some specimens, sculpture punctate or rugose; paramere obliquely truncate, narrow anteroventrally, narrower at apex than at base, length much less than 0.33 of metasoma (fig. 66); aedeagus triangular in cross section and slightly knobbed at apex but flattened at base (fig. 66); digitus short, apex scarcely longer than broad (fig. 66). Basal ring medially desclerotized, without median carinae (fig. 65).

Sathon aggeris is an unusually dimorphic species, with males more different from the female than some other *Sathon* species are from one another. However, the paratype males do have the autapotypies for the species, the completely rimulose posterior margin of the metanotum and the markedly convex T1 of the metasoma (although much less developed than the female).

Cocoon, Larva, *Hosts*.- Unknown.

***Phylogenetic Affinities*.**- *S. aggeris* is the sister species of *S. laevidorsum* .

Distribution.- Known only from the type locality.

Chorological Affinities.- The range of this species does not overlap with any other *Sathon* species. This species is the only known South American *Sathon*. It is not known if *S. aggeris* is sympatric with its Central American sister species, *S. laevidorsum*.

Paratypes.- Four males, same data as holotype, one gold coated for S.E.M.

3.5.3 *Sathon masoni* new species

Holotype.- Female, Anchorage, Alaska / 24-VII-1951. / R.S. Bigelow. [with det. label, Apanteles n. sp. falcatus / Det. W.R.M. Mason 74.] (CNC).

Derivation of Specific Epithet.- Named with pleasure for W.R.M. Mason, who first recognized this new species, and without whose guidance and pioneering work this study of *Sathon* could not have been done.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: propodeum with raised lateroapical carinae and rugosity; antennal scape concolorous with flagellum; hypopygium of female with angulate posterodorsal margin; apex of ovipositor of female with well developed subapical constriction.

Description.-

Female. *Color*. Head and mesosoma piceous; metasoma piceous with anterolateral fulvous or brown spot; antennae fulvous basally in some specimens; fore and middle legs

fulvous and darkened apically, hind leg fulvous, darkened apically and with base of coxa piceous; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially and less convex dorsally than laterally. Clypeus with dorsal margin distinct and ventral margin with rim absent or medially obscure. Face with short median carina on dorsal 0.30. Malar space with sculpture posteriorly from eye to mandible or only near mandible; groove from ventral margin of eye to anterior mandibular articulation medially or almost entirely obsolete. Oral plate evenly pigmented, dorsal margin slightly convex (fig. 77).

Mesosoma. Pronotum (fig. 68) with dorsal groove decurved and moderately foveolate; ventral groove foveolate posteriorly and broadly foveolate anteriorly, but not rugose; ventral margin sinuate; width of ventral polished band at posteroventral angle approximately four times width at collar, smooth posteriorly, not bottle shaped with sinuation of ventral groove and ventral margin not matched; pronotal disc with punctures over most of surface; discal pit obscure. Propleuron punctate posterolaterally. Mesoscutum with posterior edge of each puncture obscure, but relatively more distinct on anterior part of mesoscutum than posterior part; setae posteriorly directed anteriorly and laterally, posteromedially directed medially and posteriorly, with line of setal convergence. Prescutellar furrow (fig. 69) arcuate or irregular, but not straight, with anterior margin distinct; cross carinae nearly as high as scutellum and median carina highest in most specimens. Scutellum (fig. 70) with lunule narrower than costate area and with dorsal margin evenly convex or slightly more convex medially than laterally; costate area with costae complete, in most specimens with irregular carina extended across costae and parallel to anterior and dorsal grooves, or at least with some irregular carination between some costae; anterior groove crossed by several costae; dorsal groove wide; dorsal margin of costate area in most specimens with some sculpture or surface irregularity on polished median part of scutellum; posterior margin of scutellum with moderate median lobe. Metanotum (fig. 72) slightly convex laterally; posterior margin without rim; medial pit

sculptured, narrowed apically; lateral pits partially sculptured, wider than part of metanotum anterior to pits, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 71) with foveolation of median groove indistinct or absent, furrow distinct, but obsolete near midpit in some specimens; posterior part of metapleuron with slight sculpture on posterior 0.33, but with indistinct granular microsculpture anterior to this; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 72) punctate basally, rugose apically, with raised lateroapical carinae and rugosity; median carina on apical 0.5, with irregular surface that confluent with transverse rugosity on median propodeal area; spiracle round, separated from pleural carina by 0.5 or more of its own diameter; medioapical boss round, but with median carina widened apically in some specimens and boss appearing triangular.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and approximately 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures in longitudinal band on lateral surface and distinct on dorsal surface, but some specimens with all punctures indistinct (fig. 74).

Fore wing with Rs base longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight knob on 1A+2A, but some specimens with unpigmented trace visible part way to wing margin; 2+3Rs slightly sinuate, not decurved apically; 1Rs+M evenly slightly curved. Hind wing with Cu+cu-a moderately curved near junction with M+Cu and straight near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 73) rugosopunctate lateroapically, polished medially in most specimens but rugose in markedly sculptured specimens; apex narrower than base, with sides straight and apically convergent; apex moderately convex. T2 (fig. 73) with lateral margins obscured by rugosity; rugose, but with polished median area; apical margin sinuate, but furrow

marking margin incomplete in some specimens. T3 smooth; apex not desclerotized or whitened. T4 to T7 not desclerotized or whitened; setae scattered evenly across terga. Island oval or teardrop-shaped. Hypopygium (fig. 78) with setae concentrated basally and apically, or absent midventrally at midlength; apex entire medioventrally; posterodorsal margin angulate and joined to ventral margin at approximately 80°, in some specimens also slightly sinuate near apex. T9 approximately 2.5 times higher than wide (fig. 76). Second valvifer (fig. 76) short, barely projected into upper 0.5 of T9, apex in form of narrow bottleneck that has apodemes anteriorly and posteriorly. Third valvula (fig. 76) decurved, with ventral margin sclerotized and concave, but only slightly concave in some specimens; setae on apical 0.75 or more, only slightly more concentrated ventrally than dorsally; apex with desclerotized area small and acute or absent. Ovipositor (fig. 76) evenly shallowly decurved; slightly longer than hind tibia, with subapical constriction; basal bulb somewhat abruptly set off from shaft.

Male. Similar to female, except: some specimens with mesoscutal punctures evenly delimited on all sides, but punctures as a whole less distinct posteriorly than anteriorly; dorsal margin of scutellar costate area irregular in some specimens; metanotum without lateral convexity; penultimate fore tarsomere approximately 1.8 times long as wide; paramere obliquely truncate, narrow anteroventrally, slightly widened at apex and approximately as wide as extreme base, length much less than 0.33 of metasoma (fig. 80); aedeagus triangular in cross section throughout length and distinctly knobbed at apex (fig. 80); digitus slightly elongate (fig. 80); basal ring medially desclerotized, without median carinae (fig. 79).

Cocoon, Larva, *Hosts*.- Unknown.

***Phylogenetic Affinities*.**- *S. masoni* is the sister species of *S. cinctiformis* .

***Distribution*.**- Northwestern in Nearctic Region. I have examined specimens from the following

states and territory: **Canada**. North West Territories. **United States**. Alaska, Idaho, Minnesota.

Chorological Affinities.- The range of this species overlaps with that of *S. neomexicanus* and it has been collected at some of the same sites, but is apparently not sympatric with its sister species *S. cinctiformis*. Paucity of specimens outside of Alaska shows lack of knowledge of true southern extent of range and species status of southern specimens.

Paratypes.- 5 females, 2 males, same data as holotype. 12 females, male, Unalakleet, Alaska, 5-14-VIII-61 B.S. Heming(CNC). 9 females, male, Unalakleet, Alaska, 2-29-VIII-61 R. Madge (CNC). 22 females, Big Delta Alaska, 13-VII-1951 J.R. McGillis (CNC). 7 females, Shaw Crk. Alaska, m. 289 Rich Hwy, 11-VII-1951 Mason & McGillis (CNC). 2 females, Birch L. Alaska, near Fairbanks, 7-VII-1951 W.R.M. Mason (CNC). 2 females, Paxson Lodge Gulkana, Alaska, 4-VIII-1951 W.R.M. Mason (CNC). 2 females, King Salmon, Naknek R. Alaska, 8-VIII-1952 J.B. Hartley (CNC). 3 females, King Salmon, Naknek R. Alaska, 11-31-VIII 1952 W.R.M. Mason (CNC). 2 females, Mt. McKinley 3500', VIII-7-54 Alaska, David Townes (AEI). female, Mt. McKinley N. Pk. Alaska, F.W. Morand, Coll. 1932 (USNM). 4 females, Mile 272 Alaska, Richard Hwy 26-VIII-1951 W.R.M. Mason (CNC). female, Coleburn Ida. Bonner Co., VI-23-60 A.R. Gittins Collector (USNM). 2 females, Eaglesnest, Minn. Aug. 4 1958 collected by W.V. Balduf (USNM). female, Fort Simpson N.W.T. 15-VIII-1950 D.P. Whillans (CNC).

3.5.4 *Sathon cinctiformis* Viereck 1911.

Apanteles (Protapanteles) cinctiformis Viereck 1911: 176.

Apanteles cinctiformis; Muesebeck 1921: 526.

Sathon cinctiformis; Mason 1981: 80.

(*Apanteles cinctiformis* sensu Cole 1931 and Claassen 1921 = *Lathrapanteles papaipemae* sensu Williams 1985)

Type Material Examined.- Holotype: U.S.N.M. Cat. No. 13502. Great Falls, Virginia, June 18; collected by Nathan Banks.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: scape fulvous, lighter in color than flagellum; propodeum with lateroapical rugose tubercles or raised carinae; T1 of the metasoma markedly rugose, even in mediobasal groove.

Description.-

Female.*Color*. Head and mesosoma rufopiceous to piceous; metasoma piceous on T1 and apical terga, fulvous elsewhere, but terga darker than sterna in some specimens; antennal scape fulvous, flagelum brown; legs and third valvula fulvous.

Head. Occiput narrowly and shallowly indented medially, dorsal area concave in some specimens. Clypeus with dorsal margin obscure or slightly marked and ventral margin with reflexed rim present laterally or completely. Face with median carina on dorsal 0.4. Malar space with slightly or moderately developed sculpture near mandible; groove from ventral margin of eye to anterior mandibular articulation obscure over most of length or absent except near eye. Oral plate evenly pigmented, dorsal margin flat (fig. 90).

Mesosoma. Pronotum (fig. 81) with dorsal groove slightly to markedly decurved and foveolate; ventral groove foveolate posteriorly and with rugosity anteriorly, rugosity indistinct in some specimens; ventral margin sinuate; width of ventral polished band at posteroventral angle approximately four times width at collar, smooth posteriorly, band bottle shaped with sinuation of ventral margin and ventral groove matched, but dorsal margin of band irregular anterior to midlength; pronotal disc with punctures over most of surface; discal pit deep. Propleuron with punctures obscure posterolaterally. Mesoscutum with posterior edge of most punctures obscure, punctures almost absent posteriorly and distinct anteriorly, some specimens with punctures distinct all around; setae posteromedially directed near prescutellar furrow, posteriorly directed elsewhere, without line of setal convergence. Prescutellar furrow (fig. 82) arcuate, with anterior margin distinct; cross carinae as high as scutellum or nearly so laterally, but carinae lower medially. Scutellum (fig. 83) with lunule as wide as costate area and with dorsal margin evenly convex; costate area with costae complete or faint medially, with carina parallel to anterior and dorsal grooves, or at least with some irregular carination between some costae; anterior furrow moderately deep and crossed by several costae; dorsal groove wide; dorsal margin of costate area with some sculpture or irregularity present on polished median part of scutellum; posterior margin of scutellum with slight median lobe. Metanotum (fig. 85) slightly convex laterally; posterior margin without rim; medial pit sculptured, with irregular anteriorly divergent sides; lateral pits slightly rugose with smooth areas to almost completely rugose, approximately as wide or narrower than part of metanotum anterior to pit, with distinct anterior margin, part of metanotum anterior to pit sculptured. Metapleuron (fig. 84) with median groove distinct, foveolate except near midpit; posterior part of metapleuron with marked rugose and granular sculpture on posterior 0.4 - 0.8 and with one or several carinae as high as posterior carina and protruded on to sculptured area; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 85) punctate basally, rugose apically and with raised carinae and rugosity lateroapically; median carina on apical 0.6 - 0.9, with irregular surface confluent with slight transverse rugosity on median propodeal area; spiracle round or

broadly oval, separated from pleural carina by its own diameter, but connected to pleural carina by carina of equal height in some specimens; medioapical boss round, but some specimens angularly connected to median carina and appearing somewhat broadly triangular.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and nearly 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures obscure except for narrow longitudinal band on lateral surface and deep punctures on dorsal surface, but some specimens with punctures indistinct (fig. 87).

Fore wing with Rs base longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight bulge on 1A+2A; 2+3Rs slightly sinuate, not decurved apically; 1Rs+M straight. Hind wing with Cu+cu-a moderately curved near junction with M+Cu and nearly straight near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 86) striate-rugose medially and rugose or areolate-rugose apically and laterally; apex narrower than base, but wider subapically than base in some specimens, with sides sinuate, or straight and parallel on basal 0.75 but apically convergent on apical 0.25; apex slightly convex. T2 (fig. 86) with lateral margins obscured by rugosity; rugose, but with slight granular sculpture medially in some specimens; apical margin slightly sinuate to almost straight. T3 rugose mediobasally, sculptured area small in some specimens; apex slightly desclerotized and whitened. T4 to T7 slightly desclerotized, not whitened; setae evenly scattered across terga, but limited to a single row on T4 in some specimens. Islands oval to elongate oval. Hypopygium (fig. 91) with setae absent or scarce midventrally at midlength; apex entire medioventrally; posterodorsal margin angulate and slightly sinuate near apex, joined to ventral margin at approximately 80°. T9 approximately 2.0 times higher than wide (fig. 89). Second valvifer (fig. 89) short, barely projected into upper 0.5 of T9, apex slightly narrowed and with irregular margin dorsally. Third valvula (fig. 89) decurved, with ventral margin sclerotized and concave

over most of length; setae on apical 0.75, evenly distributed, bent tipped near apex; apex with desclerotized area triangular and emarginate at tip. Ovipositor (fig. 89) nearly straight basally but sharply decurved at apical 0.3 and nearly straight distal to that; slightly longer than hind tibia, without subapical constriction; basal bulb somewhat abruptly set off from shaft.

Male. Similar to female, except: metasoma with more apical terga and some sternites rufopiceous to piceous, scape piceous or basal half of flagellum fulvous with scape and flagellum concolorous in some specimens; metapleuron with foveolation of median groove indistinct except near base, sculpture of posterior portion of metapleuron slightly to moderately developed and present only on 0.4 of posterior part; propodeal spiracle oval and separated from pleural carina by less than its own diameter; T1 apically narrowed throughout length in some specimens; paramere obliquely truncate, narrow anteroventrally, apex slightly widened and slightly narrower than extreme base, length much less than 0.33 of metasoma (fig. 93); aedeagus triangular in cross section throughout length and distinctly knobbed at apex (fig. 93); digitus slightly elongate (fig. 93); basal ring medially desclerotized and without median carinae (fig. 92).

Cocoon, Larva, *Host*.- Unknown.

Phylogenetic Affinities.- *S. cinctiformis* is the sister species to *S. masoni*.

Distribution.- Eastern Nearctic. I have examined specimens from the following provinces and states: **Canada**. Ontario, Quebec. **United States**. Indiana, Iowa, Maryland, Michigan, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, Vermont, Virginia, Wisconsin.

Chorological Affinities.- The range of this species overlaps broadly with that of *S.*

neomexicanus, but it is apparently not sympatric with its primarily western sister species, *S. masoni*.

3.5.5 *Sathon circumflexus* new species

Holotype.- Female, Doolittle Ranch / 9800' Mt. Evans / Colo. 10-VII B.H. Poole [50 km. S.W. Denver in Clear Creek CO.] (CNC).

Derivation of Specific Epithet.- Latin, masculine, meaning curved or flexed and refering to the arc-like and markedly decurved ovipositor.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: propodeal boss thickened medially; female with ovipositor evenly decurved and semicircular; male with paramere apex wider than base and length slightly less than 0.33 of metasoma.

Description.-

Female. *Color*. Head and mesosoma piceous; metasoma piceous with anterolateral fulvous spot; antenna piceous; fore and middle legs fulvous, hind leg fulvous with coxa, apex of tibia, tarsi and in some specimens external surface of femur rufopiceous; third valvula piceous.

Head. Occiput broadly and shallowly indented medially (fig. 105). Clypeus with dorsal margin delimited laterally, but slightly less so medially, ventral margin with very slight reflexed rim. Face with median carina on upper 0.25. Malar space sculptured posteriorly near mandible; furrow from ventral margin of eye to anterior mandibular articulation complete but indistinct,

to absent near mandible. Oral plate with mediolateral pigment lines, dorsal margin convex (fig. 103).

Mesosoma. Pronotum (fig. 94) with dorsal groove straight and smooth or with few foveolations; ventral groove narrow, with foveolation faint in some specimens and without rugosity anteriorly; ventral margin sinuate; width of ventral polished band at posteroventral angle approximately five times width at collar, striate posteriorly, band bottle-shaped with sinuation of ventral margin and ventral groove matched; pronotal disc with punctures on most of surface; discal pit obscure. Propleuron with slight punctures laterally. Mesoscutum with punctures obscure; setae posteriorly directed and without line of setal convergence, but some specimens with setae posteromedially directed on notauli or posterior part of mesoscutum and then line of setal convergence present in broad, indistinct form. Prescutellar furrow (fig. 95) arcuate, shallow, with anterior margin indistinct medially in some specimens; cross carinae as high as scutellum laterally, but lower or absent medially. Scutellum (fig. 96) with lunule almost as wide as costate area and with dorsal margin slightly more convex medially than laterally, or irregular; costate area without costae medially; anterior groove crossed by several costae; dorsal groove indistinct over most of length; dorsal margin of costate area with foveolations of dorsal groove impressed in some specimens; posterior margin of scutellum with slight median lobe. Metanotum (fig. 98) laterally convex; posterior margin without rim; medial pit nearly smooth, straight sided; lateral pits entirely sculptured or with small smooth areas near medial pit, wider than part of metanotum anterior to pit, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 97) with median groove slightly foveolate, obsolete or distinct near midpit; posterior portion of metapleuron with slight sculpture on posterior 0.5 or less; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 98) punctate basally, with few wrinkles apically; median carina irregular trace near medioapical boss, but extended toward metanotum by a band of low rugosity in some specimens; spiracle oval, separated from pleural carina by its own least diameter, but connected to pleural carina by raised area as high as carina, raised area and carina low in some specimens; medioapical boss

round, thickened medially.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures obscure, less so dorsally than laterally (fig. 100).

Fore wing with Rs base as long or longer than thickness of SC + R and inserted subbasally on parastigma; 2A slight convexity on 1A + 2A; 2 + 3Rs straight or slightly curved, not decurved apically; 1Rs + M straight. Hind wing with Cu + cu-a curved near junction with M + Cu and straight near junction with 1A; SC + R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 99) smooth basally and medioapically, but rugose lateroapically and with few punctures in some specimens; apex narrower than base, sides slightly sinuate; apex moderately convex. T2 (fig. 99) with lateral margins straight or slightly concave; rugose laterally and with faint granular microsculpture at base; apical margin sinuate. T3 smooth; apex slightly desclerotized and whitened. T4 to T7 scarcely desclerotized, not whitened apically; setae evenly scattered across terga. Islands oval. Hypopygium (fig. 104) with setae absent midventrally except near apex; apex entire medioventrally; posterodorsal margin sinuate. T9 approximately 2.5 times higher than wide (fig. 102). Second valvifer (fig. 102) projected into upper 0.5 of T9, apex slightly expanded dorsal to point of third valvula attachment and with apodeme posteriorly. Third valvula (fig. 102) decurved, with ventral margin sclerotized and concave over most of length; setae on almost all of length, but concentrated apically and ventrally; apex with triangular desclerotized area which has divided apex. Ovipositor (fig. 102) evenly but markedly decurved over entire length; longer than hind tibia, without subapical constriction; basal bulb abruptly set off from shaft.

Male. Similar to female, except: foveolation of pronotal grooves almost absent in some

specimens; cross carinae of prescutellar furrow equally distinct medially and laterally in some specimens; penultimate fore tarsomere approximately 2.0 times long as wide; T1 of metasoma (fig. 101) with sides nearly straight; T2 much longer than wide at apex, with granular microsculpture obscure at base; paramere obliquely truncate, narrow anteroventrally, wider at apex than at base, length slightly less than 0.33 of metasoma (fig. 107); aedeagus triangular in cross section throughout length and distinctly knobbed at apex (fig. 107); digitus elongate (fig. 107); basal ring evenly sclerotized, with slender median carina (fig. 106).

Cocoon, Larva, *Hosts*.- Unknown.

Phylogenetic Affinities.- *S. circumflexus* is the sister species to *S. neomexicanus* + *S. falcatus*.

Distribution.- Southwestern United States. I have examined specimens from the following states: **United States**: Arizona, Colorado, New Mexico.

Chorological Affinities.- The range of this species overlaps with *S. neomexicanus* and has been collected at the some of the same localities as this species at the same time.

Paratypes.- 11 females, 2 males, Doolittle Ranch, 9800' Mt. Evans, Colo. 10-VII Collectors B.H. Poole, S.M. Clark and W.R.M. Mason '61 (CNC). Female, male, Doolittle Ranch, Mt. Evans Colo. 31-VII-1961 C.H. Mann 10,000'(CNC). 5 females, Loveland Pass W. slope 9850' 8-VIII-1961 COLO. B.H. Poole (CNC). 12 females, male, Chicago Cr. 8800' Clear Cr. Co. COLO. Aug 2, 5 and 25 Collectors B.H. Poole and C.H. Mann '61 (CNC). 4 females, West Chicago Cr. 9800' Clear Cr. Co. COLO. 11-VIII-1961 Collectors B.H. Poole and S.M. Clark (CNC). Female, Echo L. 9600' Mt. Evans COLO. July 26 1961 B.H. Poole (CNC). Female, Cameron Pass, COLO. August 18 1940, Elev. 9850ft. C.W. Sabrosky Collector (UM) 2 females, Colo. 2012

[Grizzley Creek, Lar. Co. 7-19-96] Collection C.F. Baker (USNM). Female, Colo. 2013 [Forresters Ranch. 8-3-96] Collection C.F. Baker (USNM). Female, Colo. 2061 [Hardys Ranch, North Park. 7-29-96] Collection C.F. Baker (USNM). Female, Colo. 1547 [Fort Collins. 6-7-95] Collection C.F. Baker (USNM). Female, Ariz. 2569 [San Francisco Mts., Flagstaff. 7-23-97] Collection C.F. Baker (USNM). Female, Ariz. Graham Co. Hospital Flat Pinaleno Mts. Alt. 8950' 2-VIII-1965 Hugh B. Leach (CAS). Female, Chiricahua Mts. Rustlers Park VIII-16-74 Ariz. H.&M. Townes (AEI). Female, Cimarron, N. Mex. VIII 23 '55 9500' David Townes (AEI).

3.5.6 *Sathon neomexicanus* Muesebeck 1921 (1920).

Apanteles neomexicanus Muesebeck 1921 (1920): 529.

Apanteles caudatus Muesebeck 1922: 16. Synonymy by Muesebeck and Walkley 1951: 131.

Sathon neomexicanus; Mason 1981: 78.

Type Material Examined.-

A. neomexicanus - Holotype: U.S.N.M. Cat. No. 22528, Santa Fe, New Mexico. Collected by T.D.A. Cockerell, August 14, 1895. Paratypes: 3 females, same data as Holotype. Female, Colo. 2158, Coll C.F. Baker.

A. caudatus - Paratypes: Male, Carbonate, Columbia Riv. Br. Col. Jy 7-12 '08, Alt 2600 ft. J.C. Bradley (Cornell U. Cat. No. 568.4, USNM Cat. No. 24330). Female, Mica, WASH 14 July 1918, A.L. Melander.

Diagnosis.- Adults of this species are differentiated from those of other *Sathon* species by the

following combination of character states: occiput narrowly and shallowly indented medially; propodeum smooth or with slight irregular rugosity, median carina in form of short trace or extended over most of propodeal length; 3Rs of fore wing slightly sinuate, markedly decurved near wing apex; T1 of metasoma with straight, nearly parallel sides and wide medioapical smooth area; female with ovipositor markedly longer than hind tibia; male with enlarged genital capsule, length more than depth of metasoma.

Description.-

Female. *Color*. Head and mesosoma piceous; metasoma piceous with anterolateral fulvous spot, or almost entirely fulvous except for T1, margins of T2, and apex of T9; antennae piceous; foreleg fulvous or with coxa piceous near base, middle leg fulvous or with coxa piceous near base, and hind leg fulvous with coxa piceous on basal 0.33 or more; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially (fig. 1). Clypeus with dorsal margin indistinct in some specimens, ventral margin without reflexed rim. Face with median carina on dorsal 0.33, some specimens with indistinct polished ridge on middle 0.33. Malar space sculptured posteriorly and with furrow from ventral margin of eye to anterior mandibular articulation complete, or sculptured over most of surface and groove obscured. Oral plate with mediolateral pigment lines, dorsal margin concave (fig. 117).

Mesosoma. Pronotum (fig. 108) with dorsal groove straight or slightly decurved and moderately foveolate; ventral groove foveolate throughout length, but with little or no rugosity anteriorly; ventral margin sinuate; width of ventral polished band at posteroventral angle four to five times width at collar, smooth posteriorly, band bottle shaped with sinuation of ventral margin and ventral groove matched; pronotal disc with punctures over most of surface; discal pit obscure to moderately deep and distinct. Propleuron punctate posterolaterally. Mesoscutum with punctures absent or indistinct posteriorly, distinct anteriorly; setae posteromedially

directed on notauli and near prescutellar furrow, posteriorly directed elsewhere, line of setal convergence short or absent. Prescutellar furrow (fig. 109) arcuate or nearly straight medially, with anterior margin indistinct medially; cross carinae as high as scutellum or nearly so laterally, but carinae lower medially. Scutellum (fig. 110) with lunule as wide as costate area and with dorsal margin slightly more convex medially than laterally, or irregular; costate area with costae complete, with irregular cross carinae in some specimens; anterior groove crossed by several to numerous costae, dorsal groove absent or indistinct; dorsal margin of costate area smooth; posterior margin of scutellum with slight or no median lobe. Metanotum (fig. 112) slightly convex laterally; posterior margin without rim; medial pit nearly smooth, with straight or slightly curved but anteriorly divergent sides; lateral pits rugose but with smooth areas, as wide as or narrower than part of metanotum anterior to pit, with distinct anterior margin, part of metanotum anterior to pit sculptured in some specimens. Metapleuron (fig. 111) with median groove slightly sculptured but distinct over entire length; posterior part of metapleuron with deep punctures on entire length of surface, at least on dorsal 0.5; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 112) punctate basally, with slightly developed wrinkles apically; median carina irregular trace near medioapical boss or extended over most of propodeal length; spiracle broadly oval, separated from pleural carina by less than its own least diameter; medioapical boss round.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and approximately 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures obscure except for longitudinal band on lateral surface, distinct on dorsal surface (fig. 114).

Fore wing with Rs base as long or longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight decurvature or bulge on 1A+2A and unpigmented crease; 2+3Rs slightly sinuate, decurved apically; 1Rs+M slightly curved, or in some specimens

slightly sinuate. Hind wing with Cu+cu-a moderately curved near junction with M+Cu, straight or slightly decurved near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 113) slightly rugose apically and with medioapical smooth area on middle 0.33 to 0.75; apex slightly narrower than base, with sides sinuate or slightly curved at apex; apex moderately convex, but smooth area slightly concave in some specimens. T2 (fig. 113) with lateral margins slightly curved; rugose laterally and some specimens with granulate microsculpture at base, but most of tergum smooth; apical margin markedly sinuate. T3 smooth or slightly sculptured at extreme base; apex slightly desclerotized, not whitened. T4 to T7 slightly desclerotized, not whitened; setae scattered evenly across terga, but concentrated near apex of T4 in some specimens. Islands elongate oval, lengthened posteriorly. Hypopygium (fig. 118) with setae absent midventrally over most of length; apex entire medioventrally; posterodorsal margin sinuate and with a lobe. T9 approximately 3.4 times higher than wide (fig. 116). Second valvifer (fig. 116) projected well into upper 0.5 of T9, apex knobbed and with irregular or round margin. Third valvula (fig. 116) decurved, with ventral margin sclerotized and concave over most of length; setae on apical 0.75 or more, markedly concentrated near ventral side of valvula; apex with triangular and acute desclerotized area. Ovipositor (fig. 116) decurved over most of length, but markedly more so apically than basally; approximately 2.0 times as long as hind tibia, without subapical constriction; basal bulb abruptly set off from shaft.

Male. Similar to female, except: some specimens darker than female, with anteriormost lateroterga of metasoma rufofulvous; face with median carina faint, less than 0.33 of face height in some specimens; pronotum of some specimens with some rugosity in area of junction between dorsal and ventral grooves; mesoscutum with punctures slightly developed on posterior part in some specimens; propodeum with low lateroapical rugosity in some specimens; hind coxa with band of distinct punctation broadened ventrally; T1 of metasoma with very little

sculpture and with sides evenly narrowed apically in some specimens; T2 with faint sculpture in some specimens; paramere obliquely truncate, moderately wide anteroventrally, markedly wider at apex than at base, length at least 0.33 of metasoma (fig. 121); aedeagus triangular in cross section throughout length and distinctly knobbed at apex(fig. 121); digitus elongate (fig. 121); basal ring evenly sclerotized, with convergent pair of robust median carinae (fig. 120).

Cocoon. Mass shape not known, but all cocoons with flattened and slightly translucent sides indicating close appression to other cocoons. One paratype from Santa Fe, New Mexico with two tightly bound cocoons pinned under adult specimen, both with flat and slightly translucent sides which indicates removal of other cocoons.

Larva (fig. 119). Gregarious. Hypostoma with two mandibular processes and marked hypostomal spur; mandible blade curved at apex, with irregular row of irregularly pointed teeth on apical 0.66; silk press apparently with thick integument, external and some internal details visible; labial sclerite approximately wide as high.

Hosts.- *S. neomexicanus* has been reared from undetermined Noctuidae (W.R.M. Mason, pers. comm.) and from *Protagrotis obscura* Barnes and McDunnough (R. Oetting, pers. comm.).

Phylogenetic Affinities.- *S. neomexicanus* is the sister species of *S. falcatus* .

Distribution.- Transcontinental in Nearctic Region, but apparently absent from southeastern U.S.A. (fig. 140) I have examined specimens from the following territories, provinces and states: **Canada**. Alberta, British Columbia, Labrador, Manitoba, Newfoundland, North West Territories, Ontario, Prince Edward Island. **United States**. Alaska, Arizona, California, Colorado, Idaho, Michigan, Minnesota, Montana, Nevada, New Mexico, Oregon, South Dakota, Utah, Washington, Wyoming. Apparently most abundant in southwestern U.S.A.

Chorological Affinities.- The range of this species apparently overlaps with all other North American species of *Sathon*, and specimens have been collected at some of the same localities as those of *S. circumflexus* and *S. masoni*. *S. neomexicanus* is apparently allopatric with its sister species, *S. falcatus*.

3.5.7 *Sathon falcatus* Nees von Esenbeck 1834.

Microgaster falcatus Nees von Esenbeck 1834: 175; type lost, Neotype designated by Wilkinson 1945: 133.

Microgaster equestris Haliday 1834: 242. Synonymy by Curtis 1837:116.

Apanteles equestris; Hincks 1944: 20.

Apanteles priapus Gautier & Cleu 1927: 85. Synonymy by Wilkinson 1945: 133.

Sathon falcatus; Mason 1981: 78.

Neotype.- Female, Reinhard Collection, Berlin. No. 26943. Designated by Wilkinson (1945: 133).

(*Apanteles falcatus* var. *minor* Fahringer 1938 = undetermined species of *ater*-group *sensu* Nixon 1965 and *Apanteles sp. sensu* Mason 1981)

Diagnosis.-

Female. *Color*. Head and mesosoma black; metasoma black except for fulvous area on anteriormost lateroterga, but with a rufofulvous band on apex of T3 in some specimens; legs rufofuvlous, darkened apically to rufopiceous on tarsomeres, coxae piceous to black, but some specimens fulvous at extreme apex; third valvula dark rufopiceous to black.

Head. Occiput broadly and somewhat deeply indented medially, head arcuate in dorsal aspect (fig. 134). Oral plate narrow ventrally, with mediolateral pigment lines, dorsal margin slightly convex (fig. 131).

Mesosoma. Pronotum (fig. 122) with dorsal groove straight and slightly sculptured; ventral groove narrow, with slight foveolation, but some specimens with distinct foveolation anteriorly. Mesoscutum with punctures distinct over most of surface; almost all setae posteriorly directed. Prescutellar furrow moderately to markedly arcuate (fig. 123). Scutellum with lunule wide and with markedly curved or sinuate posterior margin (fig. 124). Propodeum (fig. 126) punctate basally, smooth apically or with low rugosity, especially near median carina; median carina line of rugosity near medioapical boss or extended over most of propodeal length; medioapical boss thickened medially.

Hind coxa with punctures deep, although slightly obscured on lateral surface in some specimens (fig. 128).

Fore wing with 1Rs+M sinuate.

Metasoma. T1 (fig. 127) smooth mediobasally and in some specimens medioapically, rugose or rugosopunctate elsewhere; apex narrower than base, with sides convergent throughout length but moreso on apical 0.33 than basal 0.66, some specimens nearly as wide at apical 0.66 as at base. T2 (fig. 127) with lateral margins straight or slightly convex; rugose, but with sculpture absent medially; apical margin markedly sinuate. Hypopygium (fig. 132) with apex immarginate and posterodorsal margin angulate and somewhat sinuate. T9 approximately 3.0 times higher than wide (fig. 130). Second valvifer (fig. 130) projected well into upper 0.5 of T9, apex rounded and with distinct head set off from remainder of valvifer. Third valvula (fig. 130) more decurved apically than basally, with ventral margin concave over most of length; apex with desclerotized area small, triangular and emarginate at tip. Ovipositor (fig. 130) decurved over most of length, but markedly more apically than basally; nearly 2.0 times as long

as hind tibia, with no or slight subapical constriction; basal bulb markedly set off from shaft.

Male. Similar to female, except: trochanters infuscate, apex of hind tibia, and in some specimens all femora and apex of middle tibia, extensively infuscate; scutellum with lunule wide, but not with markedly curved or sinuate posterior margin; propodeum with some lateroapical rugosity and medioapical boss triangular in some specimens; T1 of metasoma (fig. 129) evenly narrowed apically in some specimens; paramere slightly obliquely truncate, wide anteroventrally, markedly wider at apex than at base, length at least 0.33 of metasoma (fig. 136); aedeagus with a sclerotized bar in dorsal surface (fig. 135), triangular in cross section throughout length, distinctly knobbed at apex (fig. 136); digitus elongate (fig. 136); basal ring evenly sclerotized, with a divergent pair of robust median carinae at base (fig 135).

Cocoon. Vertically arranged in tightly bound oblong mass, some cocoons on mass periphery angled relative to central cocoons; individual cocoons with flattened and slightly translucent surfaces at areas of contact with other cocoons.

Larva. (fig. 133) Hypostoma with three mandibular processes and distinct hypostomal spur; mandible blade straight at apex, with single row of straight, regular teeth on apical 0.66; silk press apparently with thick integument, external and some internal details visible; integument dorsad of each hypostoma thickened, with two faintly sclerotized bars directed posteriorly from mid-length of each hypostomal sclerite.

Hosts.- *S. falcatus* has been reared from larvae of the following species of Lepidoptera: *Noctua sp.*, *Xylophasia monoglypha* Hufn., *Eupithecia succenturiata* (L.), *Pterophorus osteodactylus* Zell., *Rhyacionia buoliana* Schiff., *Agroperina lateritia* Hufn., *Synanthedon tipuliformis* Cl. and *Hepialis humuli* L. (see Shenefelt 1972 for citations of rearing records).

Phylogenetic Affinities.- *S. falcatus* is the sister species to *S. neomexicanus* .

Distribution.- Transcontinental in the Palaearctic Region, also in Java. Published records give a range from Egypt to Sweden and from Spain to Sakhalin.

Chorological Affinities.- The range of this species overlaps with both other Palaearctic species of *Sathon*, but *S. falcatus* is the only representative of the *S. falcatus*-group in the Old World. Both *S. eugeni* and *S. lateralis* have been taken at localities where *S. falcatus* has been found. Apparently allopatric with its sister species, *S. neomexicanus*.

3.6 Taxa excluded from *Sathon*

Sathon falcatus var. *minor* Fahringer 1938.

The specimen from which this variety was described has an areolate propodeum, aciculate mesonotal punctures, a desclerotized and striate hypopygium and sparsely setose vannal lobe of the hind wing. It keys to *Apanteles ater* - group in Nixon (1965) and *Apanteles sp.* in Mason (1981).

Lathrapanteles papaipemae Muesebeck 1921 (1920).

This species was included in *Sathon* by Mason (1981) in his original description of the genus, but was removed by Williams (1985: 1963).

4. PHYLOGENETIC RECONSTRUCTION

4.1 Methods

The 53 characters of table 1 were subjected to phylogenetic analysis using the methods of Hennig (1966). A phylogenetic tree of *Sathon* species was reconstructed by analysis of the distribution of shared derived character states (synapotypies), from which a classification of *Sathon* species was derived. Phylogenetic systematics was used in order that the classification derived from the phylogeny would be maximally informative about the evolution of *Sathon* species (Farris 1979, Nelson 1973).

Character states were assigned plesiotypic or apotypic polarity using outgroup comparison of character state distributions (Farris 1982, Stevens 1980). Choice of outgroup species was made difficult by the inadequate understanding of the relationship between *Sathon* and *Choeras*. If these genera are sister groups, then *Choeras* species with relatively plesiotypic character states would be most similar to the last common ancestor of both genera and would be required as an outgroup. If *Choeras* is paraphyletic to *Sathon*, then species similar to *Sathon* species, with relatively apotypic character states, would be required. An intermediate solution was chosen to attempt to allow for both possibilities. *Choeras* species were chosen whose character states ranged from preponderantly plesiotypic to preponderantly apotypic. Six species were chosen: *Choeras tiro* Reinhard, *Choeras consimilis* Viereck, and *Choeras* sp. A, B, C and D. These six species were found to be the minimum number necessary to represent a reasonable sample of variability in *Choeras* character states, from relatively plesiotypic states to apotypic states similar to those found in *Sathon*. *Choeras* sp. D is in fact very similar in habitus to *S. lateralis*-group species, except for the retention of a fully developed, setose metanotum and a midventrally creased hypopygium.

Characters with more than one state in *Sathon* were examined in all six species of *Choeras*. Those which displayed little or no variability in *Choeras* species were polarized with the plesiotypic state in *Choeras* and in the *Sathon* species which shared this state. The alternate state or states found in *Sathon*, not shared with *Choeras*, were classified as apotypic. For some characters, more than one state was shared between the genera, but the character was still used to infer phylogeny. Here, states unique to *Sathon* species were classified as apotypic, whereas all states shared between the two genera were considered plesiotypic, since no single state could be chosen on the basis of the outgroup. Since the plesiotypic state is indicated by the letter **a** in table 1, multiple plesiotypic states are indicated by the use of primes, most commonly **a'**. Similarly, apotypic states that are considered to be independently derived in unrelated species may be designated **b** or **b'**, **c** or **c'**, *et cetera*.

4.2 Characters and States

Table 1 contains characters polarized by the methods discussed above. Character states are coded alphabetically, with state **a** plesiotypic. Character states that increase in alphabetical order are considered increasingly apotypic, although some characters exhibit loss or reduction states which are considered apotypic and are coded **-b**. Character 9 is an exception to this method. The five states, **9a** to **9e**, do not form a transformation series, but each must be coded. Also, character 28 is exceptional in that there are two states that have been coded as plesiotypic, **28a** and **28a'** (see below for discussion of characters 9 and 28). For most characters with more than two states, transformation series are implied by alphabetical order of codes. Characters are numbered in the order that they appear on the cladogram, for increased correspondence between table 1 and fig. 137.

For most characters, especially autapotypies, polarization was straightforward. Here, all six species of the outgroup had the same state, and the distribution of states within *Sathon*

was completely congruent with the reconstructed phylogeny. The discussion of these characters is minimal, since most of the pertinent information is given in table 1. Characters needing no further discussion are numbers 3, 7, 8, 13, 14, 15, 16, 17, 18, 19, 20, 21, 23, 24, 29, 31, 32, 33, 35, 36, 40, 41, 45, 48, 49, 51 and 53. Some characters with missing data points must be used with caution, but their known state distributions are otherwise congruent with the reconstructed phylogeny and their polarization relatively straightforward. These characters are numbers 1, 25, 26, 27, 30, 39, 42, 43 and 47. Characters 6 and 9, also with missing data points, require further discussion because of other problems in interpretation.

Characters that are more difficult to interpret require some discussion, including information on variability of the outgroup, polarization method and points of congruency or incongruency with the phylogeny. These characters are listed here. In the following discussion some species names are joined with a '+'. These species are considered to represent members of a monophyletic lineage.

Character 2. Hypopygium, setation. Three character states: plesiotypic -moderately setose (fig. 91)(**2a**); apotypic (two states) -setose area small (fig. 118)(**2-b**), and setose area large (fig. 18)(**2b**). Difficulty in interpretation of this character is in the variability of hypopygium structure in *Choeras*. The desclerotized, striate portion of the hypopygium is asetose in outgroup species. Thus, distribution and density of setae is dependent on the size of this area in *Choeras*, but not in *Sathon*. In two outgroup species, *Choeras* sp. C and D, this desclerotized area is limited to a midventral crease, and the distribution of hypopygial setation is comparable to *Sathon*. Apotypic increases and decreases are hypothesized from a moderately setose hypopygium. There is apparent homoplasy between *S. laevidorsum* and the *S. lateralis*-group.

Character 4. T2 of the metasoma, lateral groove shape. Three character states: plesiotypic -nearly straight (fig. 127) (**4a**); apotypic (two states) -curved at base, with T2 goblet-shaped (fig. 13) (**4b**), and obscured by rugosity (fig. 73) (**4b'**). This character was

difficult to polarize because only one outgroup species, *Choeras* sp. D, has a subtriangular T2 of the metasoma similar to that found in *Sathon*. This species has nearly straight lateral grooves. Also, state **4b'** could have been derived from either of the other states. Only congruence with the reconstructed phylogeny indicates that this state is derived from state **4a**.

Character 5. Sculpture of the lateral pits of the metanotum. Two character states: plesiotypic -completely sculptured (fig. 12) (**5a**); apotypic -partially smooth (fig. 126) (**5b**). Difference in structure of the metanotum between *Choeras* and *Sathon* causes some difficulty in polarizing this character. The metanotum of *Choeras* species is complete, with a much larger and more variably sculptured pit in the outgroup. However, the lateral pits in *Choeras* species have a groove along the posterior margin which is apparently homologus with the lateral pit of *Sathon* species. This groove is completely sculptured in the outgroup, and this is considered the plesiotypic state.

Character 6. Paramere, apex shape. Two character states: plesiotypic -rounded (fig. 22) (**6a**); apotypic -truncate (figs. 66, 121) (**6b**). The paramere of all outgroup males examined is rounded apically, except in *Choeras tiro*, where it is slightly truncate. The paramere of this species appears similar to that of *S. aggeris* (fig. 66), but is less developed. A rounded paramere apex occurs in nearly all other species of Microgastrinae exclusive of *Sathon*, and this is considered to be the plesiotypic state in *Sathon*. The truncate paramere occurring in *Choeras tiro* is considered to be an independent development.

Character 9. Second valvifer, apex shape. Five character states: plesiotypic -straight and slightly narrowed (fig. 16) (**9a**); apotypic (four states) -apically narrowed (figs. 76, 89) (**9b**), apically expanded (fig. 102) (**9c**), with sutures delimiting an apical area (fig. 130) (**9d**) and curved and anteriorly deflected (figs. 31, 34) (**9e**) (all species of *Choeras* display **9a**). For this character alphabetical order is not intended to reflect degree of apotypy, nor are any transformation series implied, although there may be one that has not been detected. Letter codes, rather than primes or negatives, were used only because of the high number of states

found. The direction of evolution of this character is not well understood. There may be unresolved homoplasy.

Character 10. Hind coxa, punctation. Four character states: plesiotypic -distinct, evenly scattered (fig. 14) (**10a**); apotypic (three states) -obscure (fig. 128) (**10b**), very indistinct or absent (fig. 44) (**10c**) and limited to a midlateral band (fig. 114) (**10d**). States **10a** to **10c** form a transformation series that is incongruent with the reconstructed phylogeny, while state **10d** could have been derived from any other state. It is possible that state **10c** is a reversal in *S. falcatus* from state **10d** found in its most closely related species.

Character 11. Metasoma color. Two character states: plesiotypic -dark, from rufopiceous to black with a white to rufofulvous anterolateral spot (**11a**); apotypic -almost entirely fulvous, except for variably developed rufopiceous to piceous areas on the base and apex of the metasoma (**11b**). The apotypic state is apparently independently derived in all three species that display it. *S. neomexicanus* is polytypic for this character, with a range of states from plesiotypic to apotypic, with intermediates.

Character 12. Propodeum sculpture. Four character states: plesiotypic -moderately developed fine wrinkles (fig. 12) (**12a**); apotypic (three states) -laterapically rugose and carinate (fig. 72) (**12b**), markedly areolate-rugose over whole surface (fig. 55) (**12b'**), and nearly smooth (figs. 27, 49) (**12-b**). The last state is independently derived in the two species that display it, while states **12b** and **12b'** form a possible transformation series that is incongruent with the reconstructed phylogeny.

Character 22. Metanotal midpit, shape. Three character states: plesiotypic -sides irregular or curved, in some specimens slightly anteriorly divergent (fig. 27) (**22a**); apotypic (two states) -sides anteriorly convergent (fig. 49) (**22b**), and sides anteriorly divergent (fig. 112) (**22-b**). An apparent transformation series extends from anteriorly divergent, through straight or curved, to anteriorly convergent (or vice versus), but neither is congruent with the

reconstructed phylogeny. The median state is considered plesiotypic, with other states independent and morphologically opposite apotypies.

Character 28. Third valvula, shape. Three character states: plesiotypic -straight (fig. 16) (**28a**), or slightly decurved (fig. 53) (**28a'**); apotypic -markedly decurved (fig. 130) (**28b**). States **28a** and **28a'** are found in both genera as two discrete states. It is not possible to confidently assign an apotypic polarity to either state because of this distribution, although one state is presumably apotypic. This character is useful, despite coding of two states as possibly plesiotypic, since state **28b** remains a useful synapotypy for those *Sathon* species that display it. Further study may give greater resolution of the evolution of this character.

Character 34. Sculpture of T1 of the metasoma. Three character states: plesiotypic - moderately rugose overall, with sculpture reduced in the mediobasal groove (fig. 13) (**34a**); apotypic (two states) -entirely markedly rugose (figs. 56, 86) (**34b**), and reduced to lateroapical punctures (fig. 50) (**34-b**). Both increases and decreases in sculpture appear from the median state. Differences between species in type of sculpture in state **34b** indicate independent origin twice.

Character 38. Ovipositor, decurvature. Four character states: plesiotypic -slightly and evenly decurved over most of length (fig. 16) (**38a**); apotypic (three states) -markedly and evenly decurved over most of length (fig. 102) (**38b**), markedly decurved at apex, slightly decurved elsewhere (fig. 116) (**38b'**), and with a sharp subapical bend, slightly decurved or straight apicad and distad of bend (fig. 89) (**38b''**). Two states appear in the outgroup, **38a** and a state similar to **38b'** but markedly less developed. Since the latter state does not appear in *Sathon*, the former state, **38a** is classified as plesiotypic. The high degree of distinctiveness among states prevents resolution of possible transformation series.

Character 44. Ovipositor length/ hind tibia length. Three character states: plesiotypic -ratio approximately 1.0 (**44a**); apotypic (two states) -ratio approximately 1.5 (**44b**), and

approximately 2.0 (**44c**). The plesiotypic state appears interspecifically variable, ranging from approximately 0.75 to 1.25 in both genera. Several possibly discrete states may be subsumed under the plesiotypic coding, but outgroup variability prevents discrimination of other apotypic states.

Character 46. Third valvula length/ hind tibia length. Two character states: plesiotypic -ratio approximately 0.75 (**46a**); apotypic -ratio approximately 1.0 (**46b**). The plesiotypic state appears interspecifically variable, ranging from approximately 0.60 to 0.85 in both genera. As for character 44, recognition of several possible apotypic states is prevented by high variability in the outgroup.

Character 50. Occiput of head, indentation. Three character states: plesiotypic -narrowly and shallowly indented (fig. 1) (**50a**); apotypic (two states) -broadly and shallowly indented (fig. 105) (**50b**), and broadly and deeply indented, head appearing arc-shaped in dorsal aspect (fig. 134) (**50c**). These states form an apparent transformation series that is incongruent with the reconstructed phylogeny, unless state **50a** in *S. neomexicanus* is a reversal.

Character 52. Hypopygium apex, shape. Two character states: plesiotypic -apex entire and pointed (fig. 118) (**52a**); apotypic -apex immarginate, flattened in lateral aspect (fig. 132) (**52b**). Both states appear in the outgroup. Emargination of the apex, however, is found in *Choeras* species with a large desclerotized and striate midventral area. *Choeras* species with this area reduced, and the hypopygium more comparable to that of *Sathon* species, display state **50a**.

Source line#
2465

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2483 **Table 1. Characters and Character States used in Phylogenetic Analysis**

2484 For discussion of characters see text. lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S.*
2485 *masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*. a or a' = plesiotypic; b or b', c, d, e = apotypic; - =
2487 unknown.
2488

2490 Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
2492										
2494 1. T9 anterior margin	b	b	b	-	-	a	a	a	a	a
2495 a = curved										
2495 b = deeply indented										
2496 2. Hypopygium setae	b	b	b	b	a	a	a	-b	-b	-b
2497 a = sparse										
2497 b = dense										
2497 -b = very sparse										
2498 3. T6+T7 sclerotization	b	b	b	a	a	a	a	a	a	a
2499 a = sclerotized										
2499 b = desclerotized										
2500 4. T2 groove shape	b	b	b	a	a	b'	b'	a	a	a
2501 a = straight										
2501 b = curved										
2501 b' = obscured										
2502 5. Metanotal lateral pit sculpture	a	a	a	b	b	b	b	b	b	b
2503 a = complete										
2503 b = incomplete										
2504 6. Paramere apex shape	a	-	-	-	b	b	b	b	b	b
2505 a = round										
2505 b = truncate										
2506 7. Third valvula sculpture	a	a	a	b	b	b	b	b	b	b
2507 a = matte, striate										
2507 b = polished, smooth										
2508 8. Hypopygium margin shape	a	a	a	b	b	c	c	b	b	b
2509 a = curved										
2509 b = sinuate										
2509 c = angulate										
2510 9. Second valvifer apex shape	a	e	e	-	-	b	b	c	a	d
2511 a = straight										
2511 b = apically narrowed										
2511 c = apically expanded										
2512 d = with sutures										
2512 e = curved										
2513 10. Hind coxa punctation	a	a	c	a	a	d	d	d	d	b
2514 a = marked										
2514 b = obscure										

Source line#
2616

2616

2616 **Table 1. Characters used in Phylogenetic Analysis (cont.)**

	Character	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
2514	c = absent										
2515	d = in midlateral band										
2516	11. Metasoma color	a	a	b	a	a	a	b	a	a-b	a
2517	a = rufopiceous										
2517	b = fulvous										
2518	12. Propodeum sculpture	a	-b	a	-b	b'	b	b	a	a	a
2519	a = wrinkled										
2519	b = lateroapically rugose										
2520	b' = areolate rugose										
2520	-b = smooth										
2521	13. Tarsal claw shape	a	a	a	b	b	a	a	a	a	a
2522	a = stout										
2522	b = elongate										
2523	14. SC+R bulb	a	a	a	b	b	a	a	a	a	a
2524	a = absent										
2524	b = present										
2525	15. Cu+cu-a curvature	a	a	a	b	b	a	a	a	a	a
2526	a = flat or curved										
2526	b = sinuate										
2527	16. Third valvula apex band	a	a	a	b	a	a	a	a	a	a
2528	a = absent										
2528	b = present										
2529	17. Sexual dimorphism	a	a	a	a	b	a	a	a	a	a
2530	a = moderate										
2530	b = marked										
2531	18. T1 convexity	a	a	a	a	b	a	a	a	a	a
2532	a = slight or moderate										
2532	b = marked										
2533	19. Metanotum rim	a	a	a	a	b	a	a	a	a	a
2534	a = absent or partial										
2535	b = complete, foveolate										
2536	20. Metapleural posterior carina	a	a	a	a	b	a	a	a	a	a
2537	a = narrow, round										
2537	b = widened, angulate										
2538	21. Propleuron sculpture	a	a	a	a	b	a	a	a	a	a
2539	a = punctate										
2539	b = striate										
2540	22. Metanotal midpit sides	a	a	a	b	b	-b	-b	-b	-b	-b

Source line#
2616

2616

2616 **Table 1. Characters used in Phylogenetic Analysis (cont.)**

Character	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
a = curved										
b = anteriorly convergent										
-b = posteriorly convergent										
23. Metanotal posterior margin	a	a	a	a	a	b	b	b	b	b
a = convex										
b = concave										
24. Midtibial inner spur length	a	a	a	a	a	b	b	b	b	b
a = long										
b = short										
25. Paramere apex width	a	-	-	-	a	b	b	c	c	c
a = narrowed										
b = slightly widened										
c = wide										
26. Digitus length	a	-	-	-	a	b	b	c	c	c
a = short										
b = elongated										
c = long, finger-like										
27. Aedeagus shape	a	-	-	-	a	b	b	b	b	b
a = oval cross-section, apex rounded										
b = triangular cross-section, apex knobbed										
28. Third valvula shape	a	a	a	a'	a	b	b	b	b	b
a = straight										
a' = apically decurved										
b = decurved										
29. Ovipositor base shape	a	a	a	a	a	b	b	b	b	b
a = gradually widened										
b = abruptly widened										
30. Second valvifer length	a	a	a	-	-	b	b	a	a	a
a = long										
b = short										
31. Ovipositor constriction	a	a	a	a	a	b	a	a	a	a
a = none or moderate										
b = marked										
32. Propodeal spiracle placement	a	a	a	a	a	b	a	a	a	a
a = close to pleural carina										
b = far from pleural carina										

Source line #
2616

2616

2616 **Table 1. Characters used in Phylogenetic Analysis (cont.)**

	Character	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
2567	33. Antennal scape color	a	a	a	a	a	a	b	a	a	a
2568	a = concolorous with flagellum										
2568	b = fulvous										
2569	34. T1 sculpture	a	a	a	-b	b	a	b	a	a	a
2570	a = moderately rugose										
2570	b = markedly rugose										
2571	-b = smooth										
2572	35. Third valvula color	a	a	a	a	a	a	b	a	a	a
2573	a = rufopiceous to black										
2573	b = fulvous										
2574	36. Third valvula seta shape	a	a	a	a	a	a	b	a	a	a
2575	a = straight										
2575	b = bent-tipped										
2576	37. Metapleural sculpture	a	a	a	a	a	a	b	a	b'	a
2577	a = slightly punctate										
2577	b = rugose										
2578	b' = markedly punctate										
2579	38. Ovipositor decurvature	a	a	a	a	a	a	b''	b	b'	b'
2580	a = even, slight										
2580	b = even, marked										
2581	b' = apically decurved										
2582	b'' = sharp subapical bend										
2583	39. Basal ring sclerotization	a	-	-	-	a	a	a	b	b	b
2584	a = medially desclerotized										
2584	b = evenly sclerotized										
2585	40. Oral plate color	a	a	a	a	a	a	a	b	b	b
2586	a = unicolorous										
2586	b = medially pigmented										
2587	41. T2 posterior margin shape	a	a	a	a	a	a	a	b	b	b
2588	a = curved										
2588	b = bisinuate										
2589	42. Paramere length	a	-	-	-	a	a	a	b	c	c
2590	a = short										
2590	b = elongated										
2590	c = long										
2591	43. Basal ring carinae	a	-	-	-	a	a	a	b	c	c
2592	a = absent										
2592	b = one, slender										

Source line#
2616

2616

2616 **Table 1. Characters used in Phylogenetic Analysis (cont.)**

Character	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
c = two, robust										
44. Ovipositor length/ hind tibia length	a	a	a	a	a	a	a	b	c	c
a = approx. 1.0										
b = approx. 1.5										
c = approx. 2.0										
45. T2 of male length	a	a	a	a	a	a	a	b	a	a
a = length = width										
b = length more than width										
46. Third valvula length/ hind tibia length	a	a	a	a	a	a	a	a	b	b
a = 0.75 or less										
b = 1.0 or more										
47. T9 height/ length	a	a	a	-	-	a	a	a	c	b
a = 2.0 - 2.5										
b = 3.0										
c = 3.5										
48. Paramere truncation shape	a	a	a	a	a	a	a	a	b	a
a = ventrally oblique										
b = dorsally oblique										
49. 3Rs apex curvature	a	a	a	a	a	a	a	a	b	a
a = straight or curved										
b = decurved										
50. Occiput indentation	a	a	a	a	a	a	a	b	a	c
a = narrow, shallow										
b = wide, shallow										
c = wide, deep										
51. Oral plate shape	a	a	a	a	a	a	a	a	a	b
a = wide ventrally										
b = narrowed ventrally										
52. Hypopygium apex shape	a	a	a	a	a	a	a	a	a	b
a = entire										
b = emarginate										
53. Paramere base shape	a	a	a	a	a	a	a	a	a	b
a = narrow										
b = wide										

2619

4.3 Reconstructed Phylogeny

The reconstructed phylogeny of *Sathon* species is given in fig. 137. Species that have more plesiotypic character states are placed toward the left side of the cladogram, while those with more apotypic states are placed toward the right, within the constraints of the branching pattern. Hence, the *S. lateralis*-group as a whole is considered more plesiotypic overall than the *S. falcatus*-group, while *S. neomexicanus* and *S. falcatus* are considered to be the most apotypic overall of all *Sathon* species. This is also reflected in the placement of species in sister species pairs, with the species to the right having more apotypic states. All apotypic states of a species not shared with the sister species or group are listed beside the branch representing that species.

Each dichotomy is supported by at least one apotypic character state. Apotypic states that support each dichotomy are listed beside the black square used to indicate apotypic states. Character numbers are as listed in table 1, along with the letter code for the state of that character which occurs at that branch. Dichotomies are given letter codes in upper case whose order approximately corresponds to the phylogenetic sequence. Generally, a greater number of apotypic states occur in dichotomies to the right of the cladogram. This is due in part to the overall apotypy of the *S. falcatus*-group relative to the *S. lateralis*-group. Also, there is accumulation of multistate characters that have their most apotypic states in *S. neomexicanus* and *S. falcatus* and form transformation series that are important indicators of phylogeny. This is shown by the appearance toward the right of characters whose numbers have appeared in more basal dichotomies.

4.3.1 Synapotypic character states

Many character states are shared among *Sathon* species and apparently contain information about their relationships. They are presented here as discussions of dichotomies, and are ranked for reliability. Characters are discussed in the order that they appear on the cladogram, in terms of support offered for each side of a dichotomy. Frequent reference to table 1 and fig. 137 will aid understanding of the following discussion.

Of the synapotypies for the *S. lateralis*-group (left side of dichotomy A), middorsal desclerotization of T6+T7 of the metasoma (character 3) is considered the most reliable. There are no missing data points and only one apotypic state. The middorsal desclerotization is either marked or very slight. For character 1, female genitalia are not completely known for all *Sathon* species, so there are missing data points. Hypopygial setation (character 2) is difficult to polarize (see above), and also displays homoplasy in the development of a densely setose hypopygium in *S. lateralis*-group species and *S. laevidorsum*. The obscured lateral grooves of the metasoma (character 4) of *S. masoni* + *S. cinctiformis* could have been derived from the state found in *S. lateralis*-group species. The pattern of evolution of this character is uncertain and its value as a synapotypy for the *S. lateralis*-group is reduced.

Both characters 5 and 7 are considered reliable synapotypies for the *S. falcatus*-group (right side of dichotomy A). Lateral pit sculpture (character 5) varies in the *S. falcatus*-group, and it is difficult to polarize states (see above), but states are distinct and there is no apparent homoplasy. Interpretation of third valvula sculpture (character 7) is straightforward. As Mason (1981) has noted, the apotypic state of third vavlula sculpture is distinctive among members of the tribe Microgastrini for those *Sathon* species that display it. For character 6, paramere apex shape, there are missing data points and some difficulty in polarization (see above). For character 8 there is a transformation series, but angulate hypopygium of *S. masoni* + *S. cinctiformis* could have been derived from the plesiotypic state of the *S. lateralis*-group. This reduces the value of the specialized hypopygium as a synapotypy for the *S.*

falcatus-group.

Only one apotypy is given for dichotomy B. The three species of the *S. lateralis*-group are very similar to one another, with *S. papilionae* and *S. eugeni* having few apotypic states, and *S. lateralis* apparently with none. *S. papilionae* + *S. eugeni* share one of the few apotypic states in *S. lateralis*-group species. Character 9, shape of the second valvifer apex, displays considerable variability. There may be unresolved transformation series and there are missing data points in those species where females were not dissected. Although this character is of the female genitalia, which seem to be important in the evolution of *Sathon* species (see sect. 4.3.4.1), the phylogenetic arrangement of the *S. lateralis*-group should be considered tentative.

Of the characters supporting the left side of dichotomy C, characters 13 and 14 are considered the most reliable. Both the elongate tarsal claws and hind wing SC+R bulb are distinctive states that are apparently uniquely derived in *S. laevidorsum* + *S. aggeris*. Character state **15b**, Cu+cu-a sinuation, is also apparently uniquely derived, but the plesiotypic state of this vein is variable in degree of curvature. Shape of the metanotal midpit (character 22) displays a three-state phenetic transformation series, but with the intermediate character considered plesiotypic. Alternate polarizations, with either anteriorly convergent or anteriorly divergent states classified as plesiotypic, would change the phylogenetic information this character contains.

Numerous characters support the right side of dichotomy C, of which character 29 is considered the most reliable. Slightly versus markedly widened ovipositor bases are distinct, and the markedly widened base is apparently uniquely derived. Character 10 is highly varied, displaying homoplasy in reduction of hind coxa punctures in *S. eugeni* and *S. falcatus*. If the limitation of hind coxa punctures to a midlateral band is assumed to be synapotypic for species on the right side of dichotomy C, then the uniformly but slightly punctate hind coxa of *S. falcatus* must be a reversal. As mentioned above, character 22, shape of the metanotal midpit, is difficult to interpret. Characters 25 to 27 are of the male genitalia, and display missing data

points. Although these characters are considered important in later dichotomies (see below), one of the species resolved by dichotomy C is missing this information. The shape of the posterior margin of the metanotum (character 23) is varied in species with the apotypic state, implying that the concave margin is labile and perhaps not uniquely derived. Character 24, length of the midtibial inner spur, is considered moderately reliable, but does display some variability of spur length in the plesiotypic state. Variability of the outgroup for character 28, third valvula shape, necessitates classification of two states as plesiotypic. This variability reduces the value of the apotypic state as a synapotypy, and incomplete resolution of state polarities may obscure homoplasy.

All of the characters on the left side of dichotomy D display some problems in interpretation. Characters 4 and 8 are considered the most reliable, although they share a similar problem in interpretation. Both the obscured lateral grooves of T2 and the angulate posterodorsal margin of the hypopygium could have been derived from either alternate state for each character. While this does not markedly affect the value of these states as synapotypies for *S. masoni* + *S. cinctiformis*, it does affect their placement relative to other species pairs. For character 9, second valvifer apex shape, the pattern of evolution of states is unclear, and although the reduced state found in *S. masoni* + *S. cinctiformis* is unlikely to be ancestral to any other state seen in *Sathon*, uncertainty is caused by the obvious lability this character displays. Character 12, propodeal sculpture, has been discussed above. The similarity of lateroapically sculptured states in *S. masoni* and *S. cinctiformis* indicates that this is a synapotypy for these species, but there is a similarity at least in trend in *S. aggeris*. Length of the second valvifer (character 30) in unknown in two *S. falcatus*-group species, and is probably functionally correlated with the narrowed and reduced apex shape found in *S. masoni* + *S. cinctiformis* (character 9).

The right side of dichotomy D is supported by nine synapotypies. The most reliable of these are binary characters 40 and 41, and multistate character 44. Also given considerable

weight are multistate characters 25, 26, 42 and 43, although there are missing data points for these characters. They are considered important because they display transformation series, whose clear set of states in character evolution give increased information on phylogeny. Although such characters appear in dichotomy C, these characters offer the most resolution in dichotomies D through F. Characters 40 and 41, oral plate color and T2 posterior margin shape, are of unique derivation and are very distinctive. The oral plate is either unicolorous or has distinct pigment lines. The posterior margin of T2 may be variably curved in the plesiotypic state, but is nearly straight, whereas the apotypic state is markedly bisinuate. Ovipositor length (character 44) is variable in the plesiotypic state, but displays a clear apotypic increase in *S. circumflexus* + *S. neomexicanus* + *S. falcatus*. Characters 25, 26, 42 and 43 are male genital characters which display obvious transformation series in spite of missing data points (table 1). Character 2, hypopygial setation, displays an apotypic reduction of setae in *S. circumflexus* + *S. neomexicanus* + *S. falcatus*, but interpretation of polarity of this character is uncertain (see above). Character 39 has missing data points and does not display a transformation series. There is some variability in degree of sclerotization of the basal ring in both states, and the more sclerotized state may be functionally correlated to character 43, presence of basal ring carinae.

The placement of *S. neomexicanus* and *S. falcatus* as sister species in dichotomy E is supported by characters of the male and female genitalia. As in dichotomy D, multistate characters with apparently clear transformation series are important, comprising four of the six characters and displaying their most apotypic states in *S. neomexicanus* + *S. falcatus*. Characters 44 and 46 are considered the most reliable. Both are characters of the female genitalia and display no missing data points. The plesiotypic states of these characters are variable, but the states classified as apotypic are distinctive. Character 47 has similar attributes, but displays missing data points. Characters 42 and 43 are of the male genitalia. They display transformation series, but are given slightly less weight because of missing data points. Ovipositor shape (character 38) displays three apotypic states in the four species considered

most apotypic overall. Although neither of the states in *S. cinctiformis* and *S. circumflexus* are similar to the apically decurved state found in *S. neomexicanus* + *S. falcatus*, there may be an unresolved transformation series, with the entirely decurved ovipositor in *S. circumflexus* derived from the apically decurved ovipositor. However, each of the three states is distinctive enough that they all show the same degree of divergence from the ancestral state, and there is no information on function to aid in hypothesizing an evolutionary sequence of states.

4.3.2 Autapotypic Character States

There are apotypic character states given for each species on the cladogram except *S. lateralis*. Some of these states are autapotypies, apparently unique to a species and derived only once. Others are apotypic states not shared by the sister species or group, but the same or similar states may be found in other *Sathon* species. These are not strict autapotypies, but have a similar function in the cladogram when differentiating between sister species and deciding position on the cladogram based on the number of apotypic states each species has.

No apotypic states were assignable to *S. lateralis* that would differentiate this species from other members of the *S. lateralis*-group. There are characters whose states are unique to *S. lateralis* within the *S. lateralis*-group (see table 3), but these could not be reliably polarized. Apotypic states in *S. lateralis* are synapotypic for the entire species group (characters 1 to 4).

S. papilionae is apotypic for character 12. The reduction of propodeal sculpture found in this species is also found in *S. laevidorsum*. This state differentiates *S. papilionae* from other *S. lateralis*-group species, but displays homoplasy.

There are two apotypic states in *S. eugeni*. In both characters, 10 and 11, there are multiple apotypic states and apparent homoplasy. In character 10, hind coxa punctation, the state in *S. eugeni* is unique in that punctures are more completely obscured than in any other

Sathon species. A possible transformation series may be seen in the moderately obscured punctation of the hind coxa of *S. falcatus*. This may be considered intermediate between the fully punctate plesiotypic state and the state in *S. eugeni*, but the resulting transformation series is incongruent with the reconstructed phylogeny. In character 11, a predominantly fulvous metanotum is shown in *S. eugeni*, *S. cinctiformis* and some specimens of *S. neomexicanus*. Each of these occurrences is considered independently evolved.

S. laevidorsum is apotypic in three characters that are plesiotypic in its sister species, *S. aggeris*. Character 16 is autapotypic. The sclerotized band within the desclerotized third valvula apex is found only in *S. laevidorsum*, and although this apex may vary in shape and size among *Sathon* species, it is always uniformly desclerotized in the plesiotypic state. Character 2 and 12 display homoplasy. The dense setation of the hypopyium of *S. laevidorsum* is apparently also a synapotypy for *S. lateralis*-group species. As mentioned above, both *S. papilionae* and *S. laevidorsum* have a relatively smooth propodeum. In addition, *S. laevidorsum* is apotypic in character 34, with a smooth metasomal T1, unlike its sister species which has a different apotypic state.

S. aggeris is apparently a very autapotypic species, considering its relatively basal placement in the *S. falcatus*-group on the cladogram. Four of the seven characters (nos. 17, 18, 20 and 21) listed for this species are autapotypies, with unique derivations. Each of the states, marked sexual dimorphism, T1 bulbosity, angulate metapleural carina and striate propleuron are distinctive and markedly differetiated from relatively invariable plesiotypic states. Propodeal sculpture (character 12) in *S. aggeris* is unique within the genus, but propodeal sculpture is varied in both *Sathon* and the outgroup. The state of character 19, rim of the posterior margin of the metanotum, can also be considered autapotypic, although a transformation series may occur if the slight rim in other *Sathon* species is considered apotypic. *S. aggeris* is also apotypic for character 34, with a markedly sculptured T1 of the metasoma that is unlike the apotypic state found in its sister species *S. laevidorsum*.

S. masoni is apotypic for characters 31 and 32. Both states are apparently unique derivations and therefore autapotypic in *S. masoni*, but the plesiotypic states of both subapical ovipositor constriction and propodeal spiracle placement are variable. Further resolution of these characters could yield other apotypic states and possible transformation series.

S. cinctiformis has apotypic states in seven characters not shared with the sister species, *S. masoni*, the greatest number found for one species. Unlike *S. aggeris* however, these are not primarily autapotypies. Only three of seven, characters 33, 35 and 36, are autapotypies. *S. cinctiformis* is one of the lightest colored *Sathon* species, as can be seen in the autapotypic fulvous color of the antennal scape (character 33) and third valvula (character 35). *S. cinctiformis* is also one of three *Sathon* species to independently develop a fulvous metasoma (character 11). *S. cinctiformis* is autapotypic in third valvula setae (character 36), with bent-tipped setae near the apex of the valvula. In character 34, the rugosity of T1 of the metasoma in *S. cinctiformis* displays some similarity to the state found in *S. aggeris*. Rugosity of the metapleuron (character 37) is unique to *S. cinctiformis*, but there is another apotypic state in *S. neomexicanus*. The apotypic decurvature of the ovipositor (character 38) in *S. cinctiformis* is superficially similar to that of *S. neomexicanus* + *S. falcatus*.

S. circumflexus is apotypic for four characters, 9, 38, 45 and 50, but only character 45, shape of T2 of the metasoma in males, is an autapotypy. Character 9, second valvifer apex shape, is highly variable, with uncertainty in ordering of states (see above). This is also true of ovipositor decurvature (character 38). Occiput indentation (character 50) displays an apparent transformation series, with the state in *S. circumflexus* intermediate between the plesiotypic state and that found in *S. falcatus*. However, this transformation series is incongruent with the reconstructed phylogeny unless the plesiotypic state in *S. neomexicanus* is a reversal.

S. neomexicanus is autapotypic for characters 48, paramere apex truncation shape, and 49, 3Rs apex curvature. The plesiotypic states of both characters are variable. Fulvous metasomal color (character 11) has apparently been evolved three times in *Sathon* and is

polytypic in *S. neomexicanus*. The markedly punctate metapleuron (character 37) of *S. neomexicanus* is unlike the apotypic state found in *S. cinctiformis*, but is not considered an autapotypy. The apotypic state of character 47, T9 height/ length, represents the most apotypic state in a transformation series.

S. falcatus is autapotypic for characters 51, 52 and 53. This species alone in *Sathon* has a ventrally narrowed oral plate, an apically emarginate hypopygium and a wide band at the base of the paramere. Other apotypic states include a state of the highly variable second valvifer apex (character 9), an apparent intermediate state in hind coxa punctation (character 10) and a deeply indented occiput (character 50). The last two characters represent states in transformation series that are incongruent with the reconstructed phylogeny.

4.3.3 Homoplasy

Characters that display homoplasy in *Sathon* have been noted above, under the discussion of characters and the reconstructed phylogeny. A brief summary is given here and in table 2. Homoplasy is considered to be present when the distribution of a state or states is incongruent with the reconstructed phylogeny, displaying parallelism or convergence. Incongruence is judged on the weight of evidence, since most of the characters in table 1 support the reconstructed phylogeny. Homoplasy is exhibited by characters 2, 10, 11, 12, 34, 38 and 50. In characters 2, 11 and 12 essentially identical apotypic states are in non-sister groups. In characters 10 and 50, apparent homoplasy involves dissimilar states that may be considered members of transformation series that are incongruent with the reconstructed phylogeny. Characters 34 and 38 have states in non-sister species that are similar in general and display similar direction of evolution, but are different in detail. This difference is assumed to indicate different origins of the states. For character 34 there is an increase of sculpture of T1 of the metasoma in two species. For character 38 there is decurvature of the ovipositor in three

species, yielding two different states.

There is a general correlation between character lability and homoplasy. Of the characters listed above, only character 11 is binary. All others are multistate. Three of four characters with four or more states display homoplasy, character 9 the exception. In this character the direction of evolution has not been well worked out. Just as there may be an unresolved transformation series in this character, there may also be unresolved homoplasy. This is apparently a straightforward correlation between frequency or ease of character change through selection or drift and likelihood that a particular state will arise more than once.

Also, there is apparently little homoplasy in characters of the genitalia. Only two characters displaying homoplasy (2, 39) are of the genitalia, though genitalia comprise 26 of 53 characters used. This lack of homoplasy is a factor in the overall reliability of genital characters as phylogenetic indicators.

At the level of taxa, common evolutionary pressures result in much homoplasy through convergent development of adaptations in unrelated species (Mayr 1963). In *Sathon*, too little is known about life histories to understand common factors that might cause homoplasy of any states in table 2. For example, the similarity of states **38b'** and **38b''** for ovipositor shape may be due to some host dependent factor. However, there are no hosts known for *S. circumflexus*, females of which display **38b''**, nor is it known what function apical decurvature serves in host finding or penetration. This inadequacy of understanding is true for both homoplasious and congruent characters.

Table 2 summarizes homoplasy in characters of table 1. Characters are listed by number, with states displaying homoplasy or incongruent transformation series and taxa involved.

Source line#
2968

2968

2975 **Table 2. Characters of of Table 1 displaying homoplasy in *Sathon* species**

2976 For explanation of characters see text. TS = transformation series, Freq. = number of times evolved.

2978

2980 Character	State	2981 Freq. or 2981 TS	Taxa displaying homoplasy
2983			
2985 2	b	2	*S. lateralis*-group and *S. laevidorsum*
2986 10	b,c	TS	*S. eugeni* and *S. falcatus*
2987 11	b	3	*S. eugeni*, *S. cinctiformis* and *S. neomexicanus*
2988 12	b	2	*S. papillonae* and *S. laevidorsum*
2989 34	b	2	*S. aggeris* and *S. cinctiformis*
2990 38	b',b''	2	*S. cinctiformis* and *S. neomexicanus* + *S. falcatus*
2991 50	b,c	TS	*S. circumflexus* and *S. falcatus*

2993

4.3.4 Evolutionary Trends

Some generalizations emerge about the evolution of *Sathon* species and the characters that vary among them. Significant features of evolution are examined at the level of changes in characters and character complexes, and at the level of species evolution.

4.3.4.1 Features of Characters and Functional Complexes

Characters of table 1 are in three main groups: female genitalia; male genitalia; and non-genital features of adult structure. Characters of the female genitalia that vary are those associated with host finding and oviposition, those of the male genitalia are associated with possible reproductive isolating mechanisms and those from the third group serve a wide variety of functions.

Female genitalia. Characters 1, 2, 7, 8, 9, 16, 28, 29, 30, 31, 35, 36, 38, 44, 46, 47 and 52 are of the female genitalia, including T9 of the abdomen and the hypopygium as a functional complex. These characters make up the largest single block from any one functional body part (*versus* sets of characters from the head, appendages or other such groupings). These characters appear in each dichotomy of fig. 137 and could support the entire cladogram without reference to any other character system. They also comprise the largest block of multistate characters in table 1 (7 of 18). Additionally, characters of the female genitalia display little intraspecific variability, and little interspecific variability in the outgroup or in *Sathon* species that have plesiotypic character states. For these reasons, characters of the female genitalia are considered very important in the evolution of *Sathon* and in the analysis of phylogenetic

relationships.

The factors involved in this divergence of female genital structures are uncertain, but host type is probably important. Mason (1981) has hypothesized that evolution of female genitalia in the Microgastrinae is related to changes in host preference. Rearing data for *Sathon* species indicate a wide range of host types, since plesiotypic species (*S. lateralis* and *S. eugeni*) are solitary parasitoids of microlepidopterans, while apotypic species (*S. neomexicanus* and *S. falcatus*) are gregarious parasitoids of macrolepidopterans. Unfortunately, no host data are known for *Sathon* species that are intermediate in structural apotypy. Information on these species might aid in understanding selective forces producing change in *Sathon* female genitalia. Length of the ovipositor, for example, is correlated with physical location of the host. Plesiotypic *Sathon* species have relatively short ovipositors and probably parasitize larvae that are exposed, or near the substrate surface (*S. papilionae* parasitism of *Papilio zelicaon* Lucas, for example). Apotypic species have relatively long ovipositors and probably parasitize more deeply hidden hosts (*S. falcatus* parasitism of *Rhyacionia buoliana* Schiff, for example). However, there are no rearings of *Sathon* species with ovipositors of intermediate length. Also, too little is known about oviposition behavior to hypothesize how hosts effect other characters, such as shape of the ovipositor apex, shape of the second valvifer, etc.

Male genitalia. Characters 6, 25, 26, 27, 39, 42, 43, 48 and 53 are of the male genitalia. These characters appear in every dichotomy in figure 137 outside of the *S. lateralis*-group (where two of three species are not known from males). Four multistate characters are of the male genitalia, with distributions of states congruent with those of the female genitalia. Despite the absence of data on *S. papilionae*, *S. eugeni* and *S. laevidorsum*, which are not known from males, the male genital complex contains much information on *Sathon* evolution, so male genital characters are considered important in analysis of relationships. As with female genitalia, interspecific variability is high, while intraspecific variability is relatively low.

Interspecific differences in male genitalia are generally regarded as functioning in reproductive isolation (Mayr 1963). Each species of *Sathon* that is known from males has a distinctive combination of plesio- and apotypic character states that make male genitalia diagnostic. This feature may indicate that mechanical reproductive isolation may be more important in *Sathon* than in other Microgastrinae where genital divergence is low.

Other characters. Genital characters comprise nearly half (26 of 53) of characters used in the reconstructed phylogeny. The remaining 27 characters are non-genital features of adult structure. No single functional complex is dominant in this third block of characters, taken in approximately equal numbers from appendages, mesosoma and metasoma, although there are few characters from the head. Most characters in this group are more intra- and less interspecifically variable than genital characters. This would indicate a lower level of normalizing selection than on complexes that perform the important tasks of reproduction and host finding. However, some groupings in this third block of characters show enough variation that they may be significant in the life histories and evolution of *Sathon* species.

Shapes of sclerites of the anterior end of the metasoma (T1 and T2) show significant variation and are the source of many useful diagnostic characters, both in *Sathon* and in the Microgastrinae as a whole (Mason 1981, Nixon 1965). In *Sathon*, shapes and sculpture of T1 and T2 also yield characters for phylogenetic reconstruction (nos. 4, 18, 34, 41 and 45. See also unpolarized character 70, table 3). The selective forces determining states of these sclerites are not understood, but differences in states may affect mobility of the metasoma, which in turn may affect oviposition or copulatory behavior.

Sculpture is a prominent feature in the structure of *Sathon* species, in areas other than T1 and T2 of the metasoma (See characters 5, 7, 10, 12, 19, 21, 34 and 37. See also unpolarized characters of table 3, nos. 55, 62, 63 and 67). In three species sculpture shows definite tendencies, for reason unknown. *S. aggeris* and *S. cinctiformis* tend to be markedly sculptured, a convergent tendency with different end results (compare figs. 55-63 with 81-88). *S.*

laevidorsum, as the name implies, tends to have reduced sculpture. The pattern of sculpture evolution is unclear, given that *S. laevidorsum* and *S. aggeris* are sister species, and that most modifications in other species appear as autapotypies or unpolarized states not shared with sister groups. Perhaps there is a component of genetic drift in sculpture changes.

4.3.4.2 Features of Taxa

The most marked phenomenon in the evolution of *Sathon* species is the difference between the *S. lateralis*- and *S. falcatus*-groups. Species of the *S. lateralis*-group are very similar to one another in habitus and display few apotypic features. There is little character change or morphological divergence between species. This is demonstrated by the overall lack of support in shared derived characters for this section of the cladogram (fig. 137). The only synapotypic feature in this section of the cladogram is for very labile character 9, and there are no unique apotypic states in any *S. lateralis*-group species. In contrast, species of the *S. falcatus*-group have numerous apotypic states. Each species has at least one autapotypy and most species have several. Species are morphologically distinct from one another, as is shown by the relatively large number of apotypic states that differentiate each species and its sister group (fig. 137).

This can be illustrated by examining multistate characters, which display the most evolution. Only the 11 multistate characters which display no missing data points (no.s 2, 4, 8, 10, 12, 22, 28, 34, 37, 38 and 50) are examined. *S. lateralis*-group species are apotypic in only four of these characters (2, 4, 10 and 12), and character change occurs only in characters 10, 12 and 19. In *S. falcatus*-group species there are apotypic states and character changes in all multistate characters, including those not listed because of missing data points.

This trend is particularly true in characters of the female genitalia. Female genitalia are rather uniform overall among *S. lateralis*-group species, but undergo markedly more evolution

in the *S. falcatus*-group. Each species of the *S. falcatus*-group is diagnosed by its combination of plesio- and apotypic states, in those species where all female genital character states are known. An examination of female genital characters without missing data points (no.s 2, 7, 8, 16, 28, 29, 31, 35, 36, 38, 44, 46 and 52) yields results similar to examination of multistate characters. In *S. lateralis* group species there is an apotypic state only in character 2 and no character changes, while in *S. falcatus*-group species there are apotypic states in all characters and change occurs in all characters except 7.

These two trends are not entirely due to greater diversity of the *S. falcatus*-group. A comparison of similar sized clades, the *S. lateralis*-group versus the other three taxon clade (*S. circumflexus* + *S. neomexicanus* + *S. falcatus*), gives the same result. Each of the three species in the latter group have an autapotypic feature, while the species of the *S. lateralis*-group have none. The initial dichotomy in the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade is supported by six synapotypies, two of which (characters 46, 47) are not exhibited in any other dichotomy. This is not true of any dichotomy within the *S. lateralis*-group. Any species in the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade differs from the others by at least four apotypic states. The maximum number for any *S. lateralis*-group species is two.

Differences between the two species groups imply a difference in the types of selective forces operating in them. Apparently, less structural divergence has been associated with speciation events in the *S. lateralis*-group. Speciation may have been accompanied by habitat or behavioral shifts that have minimally effected the structure of *S. lateralis*-group species, which we have no information on. For example, both European species, *S. lateralis* and *S. eugeni*, have been collected at the same sites and reared from *Anthophila fabriciana* (L.), but no information is available on how these species might be partitioning this common host. This kind of information is also lacking for other species in the genus.

Differences in evolution of female genitalia between the species groups may be related to importance of host shifts in speciation, since differences in female genitalia are related to differences in host use. It is possible that speciation in the *S. falcatus*-group is accompanied by larger ecological or taxonomic changes in host type than in the *S. lateralis*-group, although there are no data to support this hypothesis. The only two species of the *S. falcatus*-group for which host data are known are allopatric sister species *S. neomexicanus* and *S. falcatus*. Both attack sod-living noctuid larvae, but may do so in a different manner. *S. falcatus* parasitizes a moderately wide range of species in various habitats, and this range might be different than that of *S. neomexicanus*. *S. lateralis* and *S. eugeni* have been reared from a common host, but *S. lateralis* has been reared from a wide taxonomic range of other species, and the third member of the *S. lateralis*-group, *S. papilionae* has been reared from a macrolepidopteran. Much more rearing of *Sathon* species is necessary before a coherent explanation of species group differences can be made.

This observed difference in evolutionary trends, along with the branching pattern of the reconstructed phylogeny, forms the basis for the organization of *Sathon* into two species groups. Two monophyletic groups are defined, each supported by synapotypies and each displaying difference in degree of divergence among component species and between one another. Especially important is the difference in genital evolution between species groups. Although little has been done to describe the genitalic variation in other members of the tribe Microgastrini (Mason 1981) it appears that this divergence of genitalia is a distinctive feature of the *S. falcatus*-group.

5. PHENETIC ANALYSIS

5.1 Methods

Numerous characters that vary significantly among *Sathon* species were not used to reconstruct the phylogeny of *Sathon* because of marked lability. These characters display numerous states in both *Sathon* and the outgroup, and this is considered *a priori* evidence that these characters are more changeable than characters which show only two states, despite the possibility of undetected reversals. They display considerable variation in the outgroup, some displaying as wide a range of states or wider in the six *Choeras* species as is found in *Sathon*. Polarization of such characters was not possible with any degree of confidence. These characters, listed in table 3, also displayed a greater amount of incongruency because of their lability, among themselves and when compared as a group to the characters in table 1. This is apparently a straightforward correlation bewteen frequency of change and likelihood that a character state would arise more than once.

Whether or not such characters are useful as indicators of phylogeny, they do contain information about degree of divergence between *Sathon* species and character evolution. This kind of information is interesting when considered with reference to reconstructed phylogenetic relationships, especially when degree of divergence and proximity of phylogenetic relationship are not correlated. Therefore, these characters, along with the polarized characters, were subjected to phenetic analysis, where polarization and other evolutionary considerations are not of great methodological importance.

The characters of tables 1 and 3 are analysed with the Taxmap program, which is discussed by Carmichael and Sneath (1969). Taxmap is a computer-operated program which performs a proximity analysis of OTU's (operational taxonomic units that can be defined as

individuals, species, higher taxa, etc. In this study OTU's are *Sathon* species). It also performs a cluster analysis using very sophisticated criteria (Carmichael, George and Julius 1968). This program was used both because of its sophistication, and its ease of use and versatility. Binary, multistate unordered, multistate ordered and continuous (morphometric) characters can be used. Analysis may be unweighted, or weighted on the basis of the amount of information (approximately the number of states occurring) each character contains.

A taxometric map (fig. 138) is produced using the proximity analysis and clustering information. This is a two-dimensional representation of the clusters, with circles expressing cluster size and lines between clusters representing linkage distance. Only the closest links are displayed, with arrows on the lines indicating the nearest neighbor of each cluster. Emphasis is given to the closest links to reduce distortion occurring when multidimensional relationships are graphically reduced to two dimensions (Carmichael and Sneath 1969). The primary disadvantage of a taxometric map is that an ordination of species, such as that provided by a cladogram, is not produced. This makes a comparison of relationships between the reconstructed phylogeny and phenetic analysis more difficult, but it is compensated for by the more accurate depiction of phenetic distances between clusters. To facilitate comparison between the two methods, a diagram of phenetic linkages is displayed adjacent to the reconstructed phylogeny (fig. 139).

5.2 Characters

Characters used in phenetic analysis only are listed in table 3. Since characters in both tables 1 and 3 are used in this analysis, the characters of table 3 are numbered consecutive to those of table 1. Species are arranged in phylogenetic order to be consistent with table 1. States of characters in table 3 are given number codes, as required by the taxmap program, and states of table 1 characters are recoded numerically. States are ordered into transformation series

based on degree of morphological similarity whenever possible. For most characters in table 1, state **a** becomes state 0, state **b** becomes state 1, etc., with primes being eliminated by reordering of states or by coding independently derived states the same. Exceptions occur for characters in which there is a negative state. These characters involve degrees of development of length, sculpture, etc., where the least developed state is not considered the plesiotypic state and is coded **-b**. Here, **-b** becomes state 0, state **a** becomes state 1, state **b** becomes state 2 and so on.

An example of recoding is provided by character 12, propodeum sculpture. State **12-b** (smooth) becomes state 0, state **12a** (wrinkled) becomes state 1, state **12b** (lateroapically rugose) becomes state 2 and state **12b'** (areolate-rugose) becomes state 3. All states are ordered by degree of similarity although this has the effect of ignoring character evolution. For example, states **12b** and **12b'** are phenetically similar and increase estimates of similarity between species with these states, even though I hypothesize that they are independently derived. Recoded states for characters of table 1 are given in lines 111 to 182 in appendix 2.

Source line#
3283

3283
3284
3301 **Table 3. Characters used for Taxmap analysis**

3302 For explanation of characters see text. Characters are numbered consecutive to table 1. lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev
3304 = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*.
3306

3308 Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
3312 54. Oral plate dorsal margin	1	0	1	-	-	2	0	3	0	3
3313 0 = concave										
3313 1 = flat, desclerotized										
3314 2 = flat										
3314 3 = convex										
3315 55. Pronotal groove sculpture	1	1	1	0	1	3	3	0	2	2
3316 0 = smooth										
3316 1 = ventral groove sculptured										
3317 2 = dorsal and ventral										
3317 groove sculptured										
3318 3 = grooves foveolate										
3319 56. Ventral polished	1	0	0	0	0	0	0	1	1	1
3320 band shape										
3321 0 = ant. narrowed										
3321 1 = bottle-shaped										
3322 57. Ventral groove width	1	0	2	0	0	1	1	0	0	0
3323 0 = narrow										
3323 1 = widened										
3323 2 = wide										
3324 58. Disc seta length	1	1	0	0	0	0	0	0	0	0
3325 0 = short										
3325 1 = long										
3326 59. Disc seta distrib.	0	1	1	0	0	0	1	0	1	1
3327 0 = sparse ventrally										
3327 1 = uniform										
3328 60. Mesoscutal seta pattern	0	0	1	1	0	1	0	0	1	0
3329 0 = medially convergent										
3329 1 = post. directed										
3330 61. Prescutellar furrow width	0	0	0	0	1	2	1	0	1	1
3331 0 = narrow										
3331 1 = widened										
3332 2 = very wide										
3333 62. Prescutellar furrow	1	1	1	1	0	2	1	1	1	1
3334 sculpture										
3334 0 = medially absent										
3335 1 = medially obscure										
3335 2 = complete										

Source line#

Table 3. Characters used in Taxmap Analysis (cont.)

Character	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
63. Scutellar costae 0 = obscure medially and anteriorly 1 = obscure medially 2 = complete	1	1	1	1	1	2	2	0	2	0
64. Scutellar anterior groove margin 0 = indistinct 1 = distinct	1	0	0	0	0	1	0	1	0	1
65. Scutellar dorsal groove width 0 = narrow 1 = post. narrowed 2 = wide	1	1	1	0	1	2	2	2	2	2
66. Metasomal lateral pit shape 0 = narrow, with anterior margin 1 = wide, without anterior margin	0	1	1	0	0	1	0	1	0	0
67. Metapleural groove 0 = absent 1 = smooth 2 = foveolate	1	1	1	0	0	2	2	1	1	1
68. Propodeal spiracle shape 0 = round 1 = oval	1	0	0	0	1	0	0	1	1	1
69. Leg color 0 = unicolorous 1 = infuscate	1	1	1	1	1	0	0	0	0	0
70. T1 shape 0 = evenly narrowed, narrow 1 = evenly narrowed, wide 2 = apically narrowed 3 = widened, narrow apex 4 = widened	0	0	0	0	4	1	3	1	2	2
71. Third valvula apex size 0 = small	1	1	1	1	0	0	1	0	1	0

Source line#

3362

3362

3362 **Table 3. Characters used in Taxmap Analysis (cont.)**

Character	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
1 = large										
72. Third valvula apex shape	0	1	0	0	0	0	1	1	0	1
0 = acute										
1 = emarginate										

3365

5.3 Phenetic Affinities

Appendix 3 is a copy of the output file made by the taxmap program. This file has not been modified from its original format, since it is already organized for maximum space saving and legibility. Note that line numbers in the appendix refer to the data file and not to the text. Both weighted and unweighted analyses were performed, with very similar results. Cluster analyses are given in lines 383 to 423 (weighted) and 568 to 608 (unweighted) in appendix 3. Information used to create the taxometric map (fig. 138) is given in lines 424 to 445, using data from the weighted analysis. A linear arrangement of species was also produced, based on phenetic relationships (fig. 139), to display a comparison between phenetic and phylogenetic links.

In both analyses, the only multispecies cluster is the *S. lateralis*-group. As seen from the first number column of the tables of nearest neighbors analysis (lines 269 to 278 weighted and lines 454 to 463 unweighted), the three species of the *S. lateralis*-group are the most closely linked in the genus, more so than sister species *S. laevidorsum* + *S. aggeris* (lines 272,273 or 457,458) and *S. masoni* + *S. cinctiformis* (lines 274, 275 or 459, 460). This cluster, cluster 1, is given as the only circle of positive radius on the taxometric map (fig. 138), all other clusters being single points without radius.

In the *S. falcatus*-group each species is placed in its own single member cluster. Nearest neighbors and the taxometric map show that sister species display close phenetic similarity. However, none of these species pairs are similar enough to be clustered together when measured against the relative cohesiveness of the *S. lateralis*-group. Nearest neighbors are *S. laevidorsum* + *S. aggeris*, *S. masoni* + *S. cinctiformis* and *S. circumflexus* + *S. falcatus* with *S. neomexicanus* also closely linked to *S. falcatus*. At a lower level of linkage, *S. laevidorsum* and

S. aggeris are more similar to the *S. lateralis*-group species than to the rest of the *S. falcatus*-group, while *S. masoni* and *S. cinctiformis* are linked to *S. circumflexus* + *S. falcatus* + *S. neomexicanus* (figs. 138, 139).

Figure 139 displays the order of links in phylogenetic versus phenetic systems. Line lengths do not indicate degree of divergence in either system. Lines serve only to display the *order* in which species are connected, with information on morphological divergence given in the nearest neighbors table and the taxometric map (fig. 138). Linkage order for the phenetic system was estimated from the nearest neighbors tables. Both weighted and unweighted analyses show that links for *S. laevidorsum* and *S. aggeris* are closest with one another, then with members of the *S. lateralis*-group, then with *S. masoni* (lines 272, 273 weighted and 457, 458 unweighted). Links for *S. masoni* and *S. cinctiformis* are closest with one another, then with *S. circumflexus* and *S. neomexicanus*, then with *S. lateralis*-group species. The closest linkage of the *S. lateralis*-group species in the *S. falcatus*-group is with *S. laevidorsum* (lines 269 - 271 weighted and 454 - 456 unweighted). The closest links of species in the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade are first with one another, then with *S. masoni* + *S. cinctiformis*, then with the *S. lateralis*-group (lines 276 - 278 weighted and 461 - 463 unweighted). This is not totally congruent with the phylogenetic branching pattern (fig. 139). The phenetic similarity between the *S. lateralis*-group and *S. laevidorsum* + *S. aggeris* supports the hypothesis that the latter two species are relatively plesiomorphic within their species group, since this similarity is primarily due to symplesiomorphy (see characters of table 1, most of which display state a in the *S. lateralis*-group and *S. laevidorsum* + *S. aggeris*).

Another point of incongruence between the phylogeny and phenetic analysis is the placement of *S. circumflexus* and *S. falcatus* as nearest neighbors, with *S. neomexicanus* linked to its sister species at a greater distance than *S. circumflexus*. The phenetic distance between *S. neomexicanus* and its sister species is caused by the presence of numerous states unique to *S. neomexicanus* within the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade. These are

especially prevalent among unpolarized characters (table 3, characters 54, 60, 63, 64, 71 and 72), and may represent unique apotypic states or retained plesiomorphies. Hence, *S. neomexicanus* is phenetically divergent from *S. circumflexus* and *S. falcatus*, although there are not an exceptionally high number of apotypies listed for this species on the cladogram (fig. 137).

Most comparisons show agreement between the two methods. All other sister species and sister group relationships are supported phenetically. The order of links among *S. lateralis*-group species is the same in both phenetic and phylogenetic analyses. Based on the order of linkages, a linear ordination of species is the same between the two methods except for the placement of *S. neomexicanus* and *S. falcatus* (fig. 139). The difference in clustering between the *S. lateralis*- and *S. falcatus*-groups is the most important congruency between the phylogenetic and phenetic analyses. As stated in the preceding chapter (sect. 4.3), members of the *S. lateralis*-group display few apotypies and few character changes, with a high degree of similarity in habitus among species. Members of the *S. falcatus*-group are distinctive, with numerous autapotypies, and are easily separated from sister species. In spite of the addition of numerous unpolarized characters that display many incongruences with the cladogram, this difference in character evolution between the species groups is preserved and quantified in the phenetic analysis. Hence, the phenetic analysis supports the classification of *Sathon* species into two species groups, reinforces hypothesized relationships between species, and illustrates some features of the evolution of the genus.

6. ZOOGEOGRAPHIC ANALYSIS

A zoogeographic study is an attempt to understand patterns in the distribution of animals, and how these patterns came about (Darlington 1957). The distributions of species are examined, and correlated with past geological and climatological events that may have affected the distributions of species under study or their ancestors. The most fruitful analyses are based on reconstructed phylogenies, in which evolutionary and geographical relationships among species are both considered (Nelson and Platnick 1981). Performing this analysis on the geographical and evolutionary history of *Sathon* is difficult. Like most Braconidae, few species have been extensively collected. Ranges, the basic data of biogeographic study, are certainly inadequately known for most *Sathon* species. Most species are known from short series of specimens from one or a few localities. This makes interpretation of distribution patterns in *Sathon* uncertain. Additionally, there is no fossil record for the genus. The only fossil microgastrine known is *Eocardiochiles* Brues, a very plesiotypic genus overall, whose relationships with extant Microgastrinae are unknown. It is certainly not closely related to *Sathon*. Although the age of this fossil from Baltic amber is known (late Eocene or Oligocene) it is of little practical use in inferring a date of origin for *Sathon*. This creates a basic problem in correlating speciation events in *Sathon* with past geological or climatological events.

An understanding of the geographical distribution of groups related to a taxon is often of benefit in finding its possible area of origin (Udvardy 1969). This method is of little use in *Sathon* biogeography, however, since *Choeras* is an inadequately known, cosmopolitan genus whose phylogenetic relationship with *Sathon* is unclear (sect. 3.2). The systematics and biogeography of *Choeras* remain unstudied.

The center of origin of *Sathon* can only be inferred from the present distributions of *Sathon* species, using the assumption that the range of the ancestor of the genus is contained within or represented by the ranges of its descendant species (Darlington 1957, Udvardy 1969).

Sathon is primarily Holarctic. The only exception is *S. aggeris*, a structurally aberrant species from South America. Given that the initial speciation event in *Sathon* probably resulted in a North American ancestor of the *S. falcatus*-group and a Palaearctic ancestor of the *S. lateralis*-group, then the ancestor was either Holarctic initially or dispersed between continents after arising on one of them. The progression rule (Hennig 1966, Brundin 1966) hypothesizes that plesiotypic species are closer to the ancestral range. By this rule, the ancestor of *Sathon* would have arisen in the Palaearctic region. The most plesiotypic species in *Sathon* is the European *S. lateralis*, and the most plesiotypic species group is the primarily Palaearctic *S. lateralis*-group. Dispersal could have occurred either through the Bering land bridge or from Europe into North America, since both routes were open for long periods of time (Matthews 1979).

Alternately, the ancestor of *Sathon* may have been Holarctic. If we accept the vicariance hypothesis that the range of a species must be continuous for that species to retain its unity, and that long distance dispersal between Europe and North America was unlikely after the opening of the North Atlantic ocean (Nelson and Platnick 1981), then the ancestor of *Sathon* would have had a Laurasian distribution. The initial speciation event in the genus would have been due to the splitting of this range, perhaps by inundation of land connections between North America, Greenland and Europe. Several such connections were in existence until the Eocene, with one between Greenland and Scandinavia possibly lingering until the Miocene (McKenna 1972, Talwani and Udintsev 1977).

No matter which hypothesis is chosen, subsequent differentiation of North American and Palaearctic populations occurred, giving rise to the first speciation event of *Sathon* phylogeny (fig. 137, dichotomy A, Fig. 142).

The ancestor of the *S. lateralis*-group was probably Palaearctic, since two of the three *S. lateralis*-group species are European. The presence of *S. papilionae* in North America is probably due to dispersal. The geographical events coincident with the speciation event that

gave rise to *S. lateralis* and the ancestor of *S. papilionae* + *S. eugeni* are unknown. *S. lateralis* and *S. eugeni* are broadly sympatric. All *S. lateralis*-group species occur in areas where habitat distributions have been markedly affected by Pleistocene glaciations (Turekian 1971) and geographical evidence of the initial speciation event has probably been obscured by these range fluctuations. The distribution of *S. papilionae* on the west coast of North America leads to the speculation that the ancestor of *S. papilionae* + *S. eugeni* may have dispersed to North America via the Bering land bridge. This connection existed for a long period of time, from the Late Cretaceous to the Pliocene, and again in the Pleistocene (Hopkins 1967), so an approximate date for the invasion of the *S. lateralis*-group into North America cannot be given. Subsequent inundation of the Bering Strait, resulting in the isolation of Nearctic and Palaearctic populations, would have given rise to *S. papilionae* and *S. eugeni*. This hypothesis leads to the prediction that further collecting in the eastern Palaearctic region might reveal the presence of *S. eugeni* or other *S. lateralis*-group species closely related to *S. papilionae* which are currently unknown. This would fill in the rather wide geographical gap between western Europe and Alaska, an area from which no specimens of *S. lateralis*-group species are known.

The ancestor of the *S. falcatus*-group appears to have been Nearctic. Five of seven known *S. falcatus*-group species occur in North and Central America. This includes *S. laevidorsum*, the most plesiotypic species overall in the *S. falcatus*-group. *S. laevidorsum* has the fewest apotypic character states of any *S. falcatus*-group species (table 1), and is very similar in habitus to *S. lateralis*-group species. Presence of *S. falcatus* group species on other continents is apparently due to dispersal.

The first speciation event in the *S. falcatus*-group may have been caused by north-south vicariance in North America (including México). This would result in a southern ancestor of *S. laevidorsum* + *S. aggeris*, and a northern ancestor of the remainder of the *S. falcatus*-group. This was apparently followed rather quickly (in geological time) by the dispersal of the southern species into South America, either by island hopping or over the

Isthmus of Panamá once this was established in the Pliocene (Rosen 1975, Raven and Axelrod 1975). Another vicariant event may have occurred relatively soon afterward, giving rise to *S. laevidorsum* in Central America and *S. aggeris* in South America. This may be related to the movement of the Caribbean islands to their present positions from a bridging position in the area of the present-day isthmus (Rosen 1975). The relative antiquity of these events is indicated by overall plesiotypy of these two species in the balance of their characters. Also, the large number of autapotypies superimposed on a plesiotypic ground plan in *S. aggeris* suggest long isolation from other *Sathon* species, assuming all evolutionary rates to be equal. Support for this hypothesis might be gained if the *Sathon* fauna of South America were more intensively studied. It would be expected that speciation in South America would have kept pace with that in North America if the ancestor of *S. aggeris* had been isolated for a long time. The result would be a monophyletic lineage related to *S. aggeris*, of which *S. aggeris* is the only known representative. The braconid fauna of South America is very inadequately known, and the possibility of the existence of unknown *Sathon* species is probably quite high.

The northern fragment of the *S. falcatus*-group ancestor gave rise to two species in North America, the ancestor of *S. masoni* + *S. cinctiformis* and the ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus*. The geographical component of this speciation is obscure. All North American species have probably undergone considerable range fluctuations during Pleistocene glaciations, which may have concealed vicariance events. Additionally, one of the extant results of North American speciation events, *S. neomexicanus*, has become transcontinental since the last glaciation, establishing sympatry with all North American species. This further obscures geographic patterns for those speciation events which had a geographical component. The only piece of information that can be noted is that both *S. circumflexus* and *S. neomexicanus* occur in the American southwest (*S. circumflexus* exclusively so), while neither *S. masoni* or *S. cinctiformis* occur there. Possibly the ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus* arose in southwestern United States as the result of some range division.

A habitat shift may also have been involved, although information supporting this is scanty. While no information is available for *S. masoni*, there are specimens of its sister species, *S. cinctiformis*, with label data indicating collection at several localities from marshy areas dominated by sedges. In contrast, specimens of both *S. circumflexus* and *S. neomexicanus* have been collected from meadows, with a preference for high altitudes or high latitiudes. *S. neomexicanus* has been reared from grass-eating noctuids. An east-west vicariance dividing the range of an apparently transcontinental ancestral species may also have occurred, resulting in a southwestern, meadow-living ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus* and an eastern, marsh-living ancestor of *S. masoni* + *S. cinctiformis*. Unfortunately, the ancestral habitat is unknown. There is little information on habitat preference for plesiotypic *S. falcatus*-group species. *S. laevidorsum* and *S. aggeris* were taken from high-altitude localities in México and Ecuador that may have no resemblance to habitats of North American species. Therefore, it is difficult to state whether the meadow or marsh habitat was ancestral, and lack of information on ecological plasticity prevents understanding of how useful such limited habitat information might be. Certainly several species of *Sathon*, among them *S. falcatus*, have wide ranges of host preference. This may be an indicator of ecological plasticity in *Sathon* species.

The current distribution of sister species *S. masoni* and *S. cinctiformis* display apparent refugial effects. *S. cinctiformis* is a primarily southeastern species, which probably survived the last glaciation south of the ice. *S. masoni* is a northwestern species found primarily in Alaska, although collecting of this species has been too inadequate to make firm statements about the southern limits of its range. *S. masoni* appears to have survived the last glaciation in the Beringian refugium (Matthews 1979), with subsequent dispersal southward at the end of the Wisconsinan glaciation period. These two species may be the result of an east-west vicariance event, perhaps related to climatic fluctuation. Refugial isolation of two populations of the ancestor may have been responsible for speciation, but since several glacial events have been hypothesized for North America (Turekian 1971) it is difficult to assign a date to this

occurrence.

Nothing is known about the geographic events, if any, involved in the separation of the ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus* into two species. *S. circumflexus* and *S. neomexicanus* are site-sympatric, and the range of *S. circumflexus* is entirely contained within the range of *S. neomexicanus*. It is not known why *S. neomexicanus* could be so ecologically plastic as to be found over most of Canada and the United States but *S. circumflexus* be limited to three southwestern states. *S. falcatus*, the other member of this clade, is also transcontinental in the Palaearctic region. Apparently, the ancestor of *S. neomexicanus* + *S. falcatus* had this trait of vagility and adaptability that is not found in its sister species *S. circumflexus*, assuming that there is no collecting bias. A difference in range of host preference may be involved, but there is no evidence to support this possibility.

The presence of *S. falcatus* in the Palaearctic region is probably due to dispersal. The large number of apotypic states shared by *S. neomexicanus* + *S. falcatus* indicates a long common history, and the dispersal of the ancestor of *S. neomexicanus* + *S. falcatus* into Europe is probably the most recent event in the geographic history of the genus. It seems very likely that this dispersal occurred long after the loss of a land connection between North America and Europe, and that dispersal likely occurred through Beringia. It is not known, however, whether this dispersal occurred in the Pliocene or more recently, during the Pleistocene. Inundation of the Bering Strait would result in speciation and the modern distributions. Both *S. neomexicanus* and *S. falcatus* are widely distributed in their respective continents, appearing quite capable of extensive range enlargement. As with the dispersal of *S. papilionae* into North America, an exact date for the reverse dispersal of the ancestor of *S. falcatus* is not known.

The above discussion shows that much more information is needed about ranges, habitat requirements and hosts before workable zoogeographic hypotheses can be proposed. Speciation need not always be accompanied by changes in range, especially in parasitic forms

where host preferences form an important aspect of life history. The effects of refugia and pleistocene climatic fluctuations may have been a dominant factor in *Sathon* distributions. These factors have had their effects over the entire globe, even in tropical regions (Prance 1982). A better understanding of host preferences and ecological requirements may allow hypotheses on which speciation events in *Sathon* may have had geographical causes and which might be attributed to other agents. Also, this type of information may aid in understanding how ranges of *Sathon* species were effected by climatic fluctuations, and how modern ranges might be related to ancestral ones. Without such information, the scenario presented above is a very tentative estimate.

7. CONCLUSION

This thesis is a preliminary study of *Sathon* Mason. The genus has been doubled in size in this study, with several species known from very little material. There is still much information to be gathered about the species, and several problems to be solved.

More information is needed about immatures and host preferences. The larvae of *Sathon* species display differences in features of the head capsule, variations in prominence of the silk press, teeth of the mandible and shape of the head capsule sclerites. They may be gregarious or solitary, and fragmentary evidence suggests different ranges of host species for plesiotypic versus apotpyic species. Information about host preference and immatures is available only for *S. lateralis*, *S. eugeni* and *S. falcatus*, with one host record each for *S. papilionae* and *S. neomexicanus*. No larval exuviae are known for *S. papilionae*. Therefore, there is information for the most plesio- and apotypic species in *Sathon*, but none for intermediate species where transformation series may exist. Much rearing of parasitized hosts is necessary to gain enough information to be useful in a systematic study, since characters based on natural history are unknown for too many *Sathon* species.

A very basic task that must be done is further collection of *Sathon* specimens. This genus has been inadequately collected in the past because of the small size of species (2 - 4mm) and their generally dark and unspectacular coloration. Specimens must be swept with an extra-fine mesh insect net or trapped with a malaise or other permanently installed trap that is effective in catching flying insects. Distributional data are fragmentary to essentially non-existant for most *Sathon* species, and habitat preferences are almost unknown. Rigorous analysis of historical geography of *Sathon* species must await much more intensive collecting, especially in the poorly known Neotropical region.

Some problems needing solution require more thorough collection of even such a relatively well known region as North America. Two examples are available. I have mentioned

above the difference in habitus between northern and southern specimens of *S. masoni*. This geographic variation remains unanalysed because of a dearth of material of this species outside of Alaska. *S. masoni* has been collected from only one locality in Canada, Fort Simpson N.W.T. Much collecting must be done in the middle and southern parts of the range of *S. masoni* before the significance of the geographic variation currently seen can be understood. *S. papilionae* provides a similar problem. This species is known from only two localities, and the two paratypes from Cold Bay, Alaska display several character state differences from the holotype from Clayoquot. Whether these differences are significant or not cannot be determined from a sample size of three.

Perhaps the most important problem needing resolution is the nature of the relationship between *Sathon* and *Choeras*. The possible paraphyly of *Choeras* relative to *Sathon* carries the attendant possibility that the two species groups of *Sathon*, which have been shown above to be markedly different from each other, may be independently derived from some *Choeras* ancestor. Distributions of character states in apotypic, primarily undescribed species of *Choeras* must be examined before the status of *Sathon* can be changed. It is hoped that this study will facilitate any future attempts at understanding the relationships between *Sathon* and *Choeras* and the relationships and evolution of *Sathon* species.

8. FIGURES

A basic set of figures is given for each *Sathon* species, covering each body part that can be used for diagnosis. Differences in arrangements among species reflects different practical considerations (sect. 2.2.3), or illustration of diagnostic characters. Groups of figures for each species are arranged in the order that the species appear in the taxonomic treatment, except for figs 1 - 7. These are semidiagrammatic drawings of *S. neomexicanus* body parts which are used only as a guide to stucture names and measurement methods.

Figures 1 to 7. Illustration of measurements. Body parts of *S. neomexicanus* drawn semidiagrammatically with all setae removed except in figure 7.

Figure 1. Head, dorsal aspect. Semidiagrammatic. HW = head width; HL = head length; AOD = anterior ocellar diameter; LOL = lateral ocellar line; LOD = latral ocellar diameter; OOL = ocellar-ocular line; POL = posterior ocellar line.

Figure 2. Head, frontal aspect. Semidiagrammatic. F = frons; H = clypeus height; L = labrum; W = clypeus width.

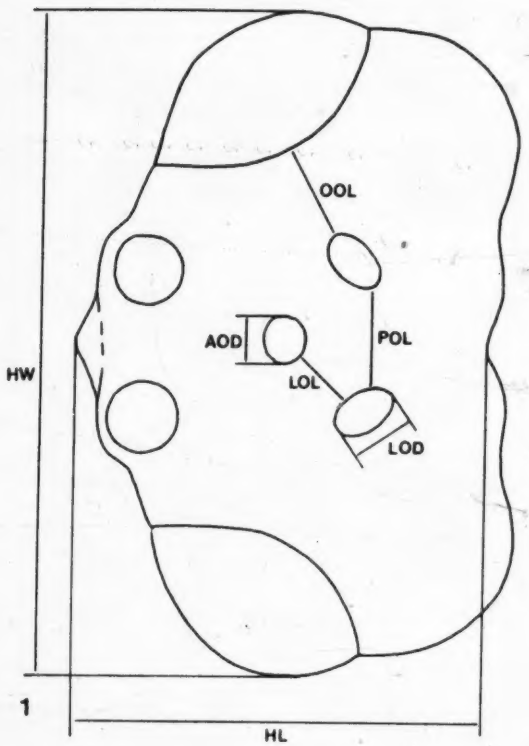
Figure 3. Hind leg. Semidiagrammatic. HCL = hind coxa length; HTL = hind tibia length.

Figure 4. Apical foretarsomeres. Semidiagrammatic. L = length of penultimate foretarsomere; W = width of penultimate foretarsomere.

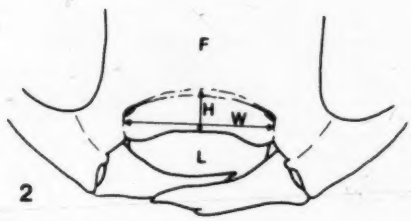
Figure 5. Apical flagellomeres. Semidiagrammatic. L = length of penultimate flagellomere; W = width of penultimate flagellomere.

Figure 6. Wing venation. Semidiagrammatic. Names and approximate measuring points of wing veins used in descriptions.

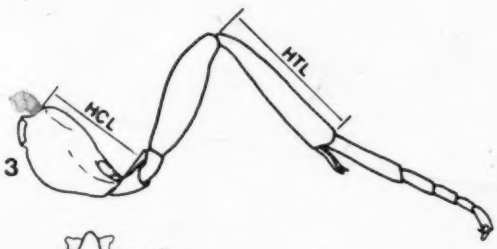
Figure 7. Third valvula. Semidiagrammatic. 3VL = length of third valvula.


OOL
AOD
POL
LOL
LOD
HW
HL

1


F
H
W
L

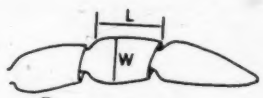
2


HTL
HCL

3

W
L

4


L
W

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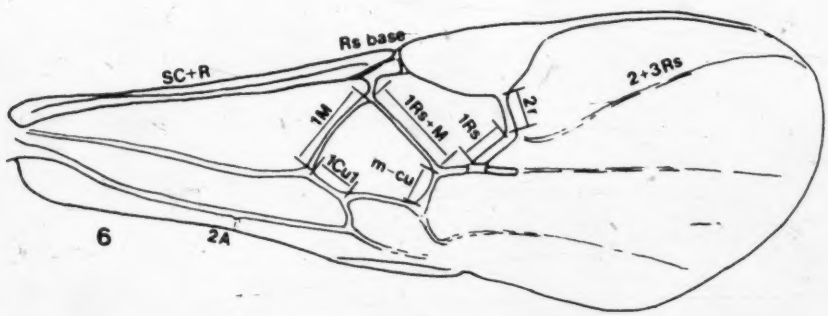
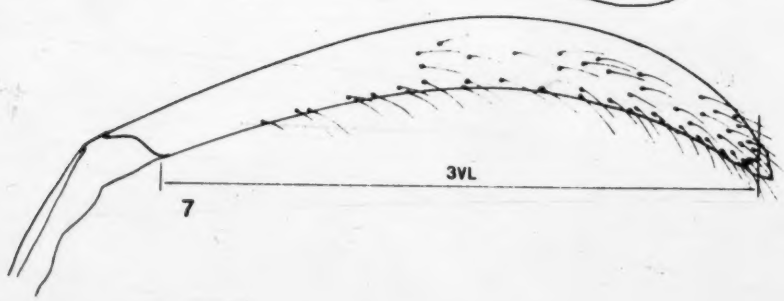

Rs base
SC+R
1M
1Rs+M
1Rs
2+3Rs
1Cu1
m-cu
2A

6


3VL

7

Figures 8 to 15. S.E.M. photographs of *S. lateralis* female. Scale bars = 0.2mm.

Figure 8. Pronotum of *S. lateralis*. In lateral aspect. C = collar; D = disc; DG = dorsal groove; VG = ventral groove; VPB = ventral polished band.

Figure 9. Prescutellar furrow of *S. lateralis*. In dorsal aspect. Arrow indicates furrow

Figure 10. Scutellum of *S. lateralis*. In dorsolateral aspect. Sl = scutellum; Slca = scutellar costa.

Figure 11. Metapleuron of *S. lateralis*. In lateral aspect. MG = metapleural groove.

Figure 12. Metanotum and propodeum of *S. lateralis*. In dorsal aspect. M = metanotum; MP = medial pit of metanotum; LP = lateral pit of metanotum; P = propodeum; PS = propodeal spiracle.

Figure 13. Anterior end of metasoma of *S. lateralis*. In dorsal aspect. T1 = first tergum of metasoma; T2 = second tergum of metasoma.

Figure 14. Hind coxa of *S. lateralis*. In lateral aspect.

Figure 15. Meso- and metasoma of *S. lateralis* male. In dorsal aspect. M = metanotum; P = propodeum; Mt = metasoma.

8
12

Figures 16 to 22. Line drawings of *S. lateralis* male and female. Scale bars = 0.5mm.

Figure 16. Female genitalia of *S. lateralis*. In lateral aspect. BB = basal bulb of ovipositor; T9 = ninth tergum of abdomen; Va3 = third valvula; Vf2 = second valvifer.

Figure 17. Oral plate of female *S. lateralis*. In anterior aspect.

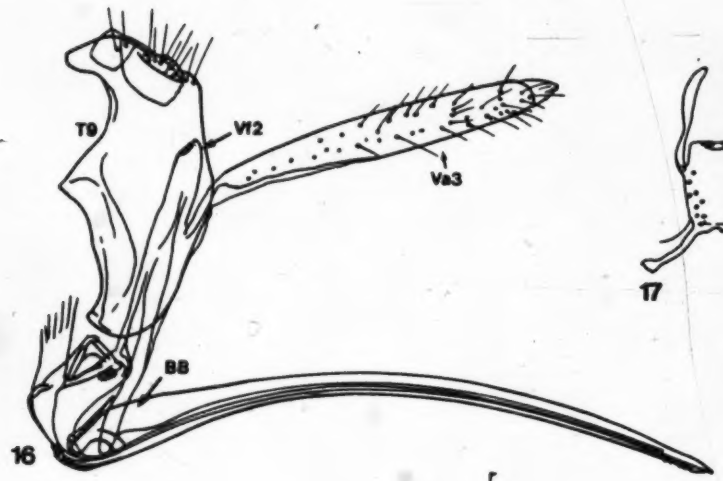
Figure 18. Hypopygium of *S. lateralis*. In lateral aspect. A = apex; PM = posterodorsal margin.

Figure 19. Head capsule of *S. lateralis* larva. In anterior aspect. Hst = hypostoma; LS = labial sclerite; Md = mandible; SP = silk press.

Figure 20. Apex of metasoma of *S. lateralis* female. In dorsal aspect. T5, T6, T7 = fifth through seventh tergum of metasoma.

Figure 21. Male genital capsule of *S. lateralis*. In dorsal aspect. Volsellae removed A = aedeagus; BR = basal ring; P = paramere.

Figure 22. Male genital capsule of *S. lateralis*. In lateral aspect. Volsellae except digitus removed A = aedeagus; BR = basal ring; D = digitus; P = paramere.



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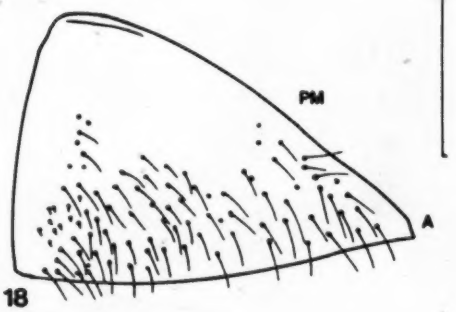

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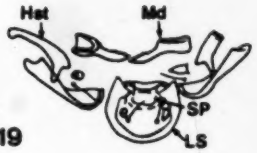

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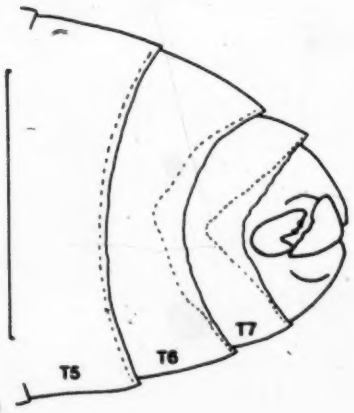

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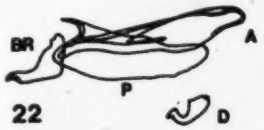

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Figures 23 to 30. S.E.M. photographs of *S. papilionae* female. Scale bars = 0.2mm except fig. 30 where scale bar = 0.05mm.

Figure 23. Pronotum of *S. papilionae*. In lateral aspect.

Figure 24. Prescutellar furrow of *S. papilionae*. In dorsal aspect.

Figure 25. Scutellum of *S. papilionae*. In dorsolateral aspect.

Figure 26. Metapleuron of *S. papilionae*. In lateral aspect.

Figure 27. Metanotum and propodeum of *S. papilionae*. In dorsal aspect.

Figure 28. Anterior end of metasoma of *S. papilionae*. In dorsal aspect.

Figure 29. Hind coxa of *S. papilionae*. In lateral aspect.

Figure 30. Third valvula of *S. papilionae*. High magnification displaying striate microsculpture.

Figures 31 to 33. Line drawings of *S. papilionae* female. Scale bars = 0.5mm.

Figure 31. Female genitalia of *S. papilionae*. In lateral aspect.

Figure 32. Oral plate of *S. papilionae*. In anterior aspect.

Figure 33. Hypopygium of *S. papilionae*. In lateral aspect.

Figures 34 to 37. Line drawings of *S. eugeni* female. Scale bars = 0.5mm.

Figure 34. Female genitalia of *S. eugeni*. In lateral aspect.

Figure 35. Oral plate of female *S. eugeni*. In anterior aspect.

Figure 36. Hypopygium of *S. eugeni*. In anterior aspect.

Figure 37. Head capsule of *S. eugeni* larva. In anterior aspect.

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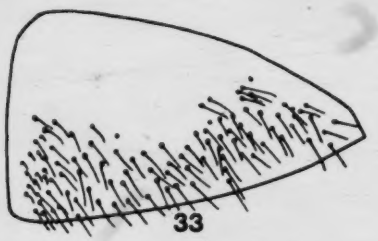
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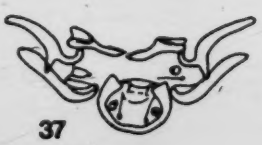
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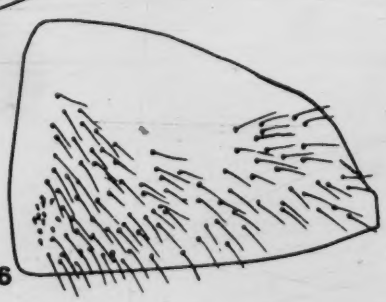
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Figures 38 to 44. S.E.M. photographs of *S. eugeni* female. Scale bars = 0.2mm.

Figure 38. Pronotum of *S. eugeni*. In lateral aspect.

Figure 39. Prescutellar furrow of *S. eugeni*. In dorsal aspect.

Figure 40. Scutellum of *S. eugeni*. In dorsolateral aspect.

Figure 41. Metapleuron of *S. eugeni*. In lateral aspect.

Figure 42. Metanotum and propodeum of *S. eugeni*. In dorsal aspect.

Figure 43. Anterior end of metasoma of *S. eugeni*. In dorsal aspect.

Figure 44. Hind coxa of *S. eugeni*. In lateral aspect.

38

Figures 45 to 52. S.E.M. photographs of *S. laevidorsum* female. Scale bars = 0.2mm.

Figure 45. Pronotum of *S. laevidorsum*. In lateral aspect.

Figure 46. Prescutellar furrow of *S. laevidorsum*. In dorsal aspect.

Figure 47. Scutellum of *S. laevidorsum*. In dorsolateral aspect.

Figure 48. Metapleuron of *S. laevidorsum*. In lateral aspect.

Figure 49. Metanotum and propodeum of *S. laevidorsum*. In dorsal aspect.

Figure 50. Anterior end of metasoma of *S. laevidorsum*. In dorsal aspect.

Figure 51. Anterior end of metasoma of *S. laevidorsum*. In lateral aspect.

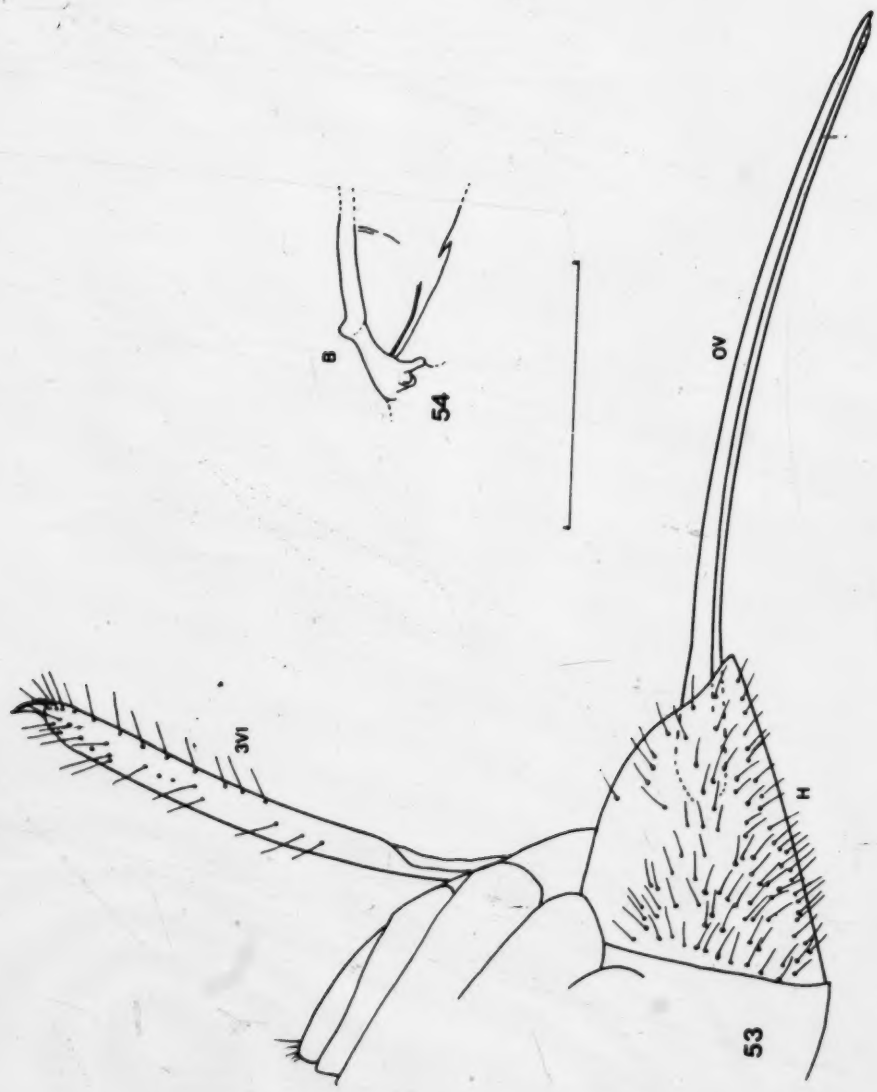
Figure 52. Hind coxa of *S. laevidorsum*. In lateral aspect.

45
52

Figures 53 to 54. Line drawings of *S. laevidorsum* female. Scale bar = 0.5mm

Figure 53. Apex of metasoma of *S. laevidorsum*. In lateral aspect. H = hypopygium; 3VL = third valvula; OV = ovipositor.

Figure 54. Anterior edge of right hind wing of *S. laevidorsum*. In anteroventral aspect. B = bulb on SC+R.


B
54
OV
3VI
H
53

Figures 55 to 60. S.E.M. photographs of *S. aggeris* female. Scale bars = 0.5mm.

Figure 55. Metanotum and propodeum of *S. aggeris*. In dorsal aspect.

Figure 56. Anterior end of metasoma of *S. aggeris*. In dorsal aspect.

Figure 57. Anterior end of metasoma of *S. aggeris*. In lateral aspect. T1 = first tergum of metasoma.

Figure 58. Hind coxa of *S. aggeris*. In lateral aspect.

Figure 59. Metanotum and propodeum of *S. aggeris* male. In dorsal aspect.

Figure 60. Anterior end of metasoma of *S. aggeris* male. In dorsal aspect.

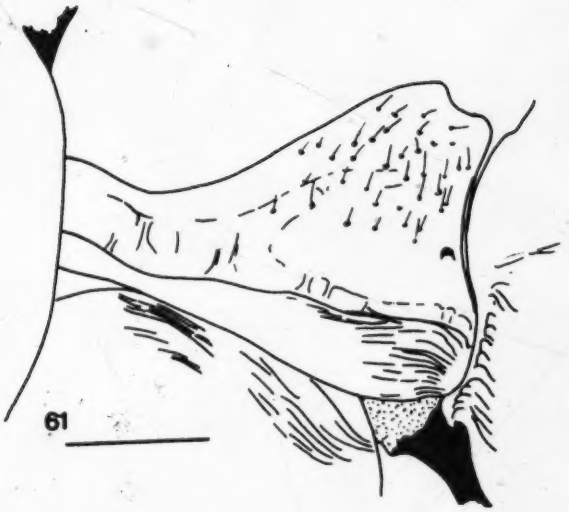
58

Figures 61 to 63. Line drawings of *S. aggeris* female from S.E.M. photographs. Scale bars = 0.2mm. Setae ommited except on pronotal disc, fig. 61.

Figure 61. Pronotum of *S. aggeris*. In lateral aspect.

Figure 62. Prescutellar furrow of *S. aggeris*. In dorsal aspect.

Figure 63. Scutellum of *S. aggeris*. In dorsolateral aspect.



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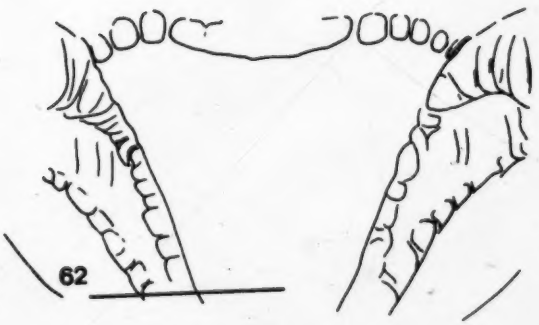

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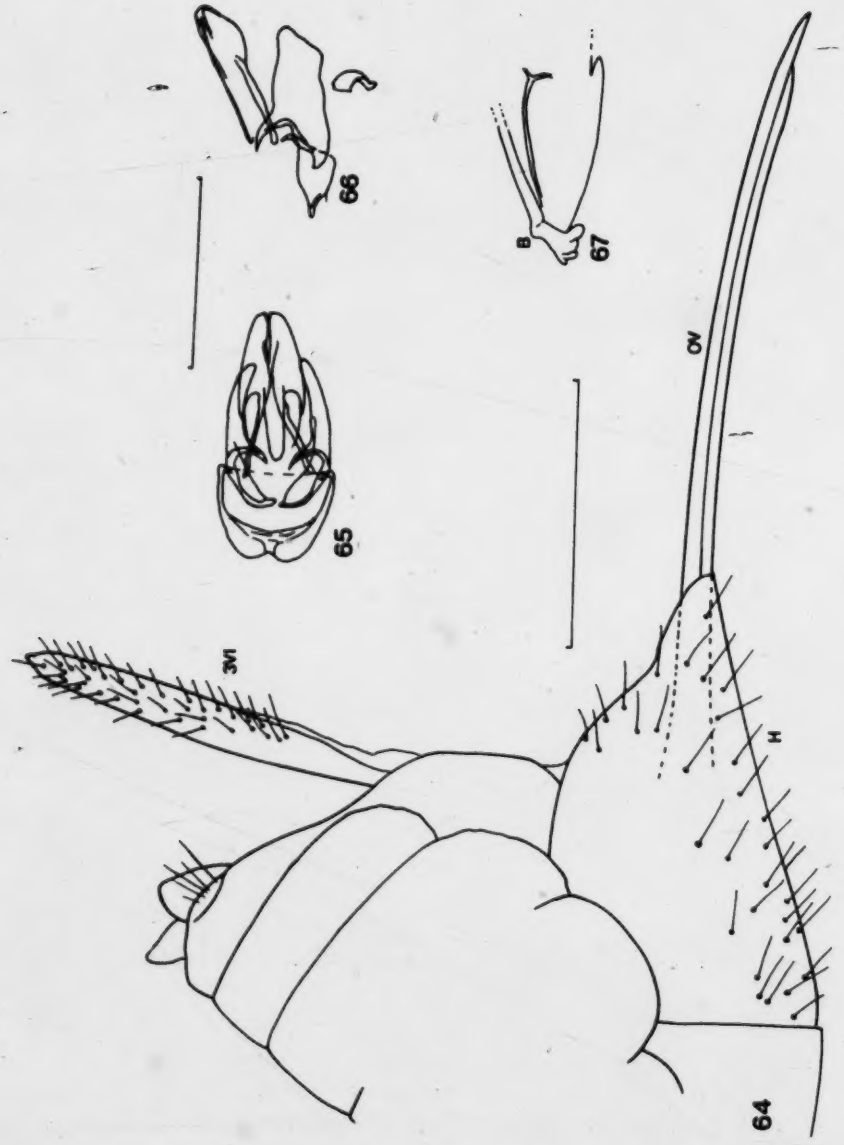
Figures 64 to 67. Line drawings of *S. aggeris* male and female. Scale bars = 0.5mm.

Figure 64. Apex of metasoma of *S. aggeris*. In lateral aspect. H = hypopgium; 3VL = third valvula; OV = ovipositor.

Figure 65. Male genital capsule of *S. aggeris*. In dorsal aspect. Volsellae removed.

Figure 66. Male genital capsule of *S. aggeris*. In lateral aspect. Volsellae except digitus removed.

Figure 67. Anterior edge of right hind wing of *S. aggeris*. In anteroventral aspect. B = bulb on SC+R.


66
67
B
65
OV
3VI
H
64

Figures 68 to 75. S.E.M. photographs of *S. masoni* female. Scale bars = 0.2mm.

Figure 68. Pronotum of *S. masoni*. In lateral aspect.

Figure 69. Prescutellar furrow of *S. masoni*. In dorsal aspect.

Figure 70. Scutellum of *S. masoni*. In dorsolateral aspect.

Figure 71. Metapleuron of *S. masoni*. In lateral aspect.

Figure 72. Metanotum and propodeum of *S. masoni*. In dorsal aspect.

Figure 73. Anterior end of metasoma of *S. masoni*. In dorsal aspect.

Figure 74. Hind coxa of *S. masoni*. In lateral aspect.

Figure 75. Meso- and metasoma of *S. masoni* male. In dorsal aspect.

74

Figures 76 to 80. Line drawings of *S. masoni* male and female. Scale bars = 0.5mm.

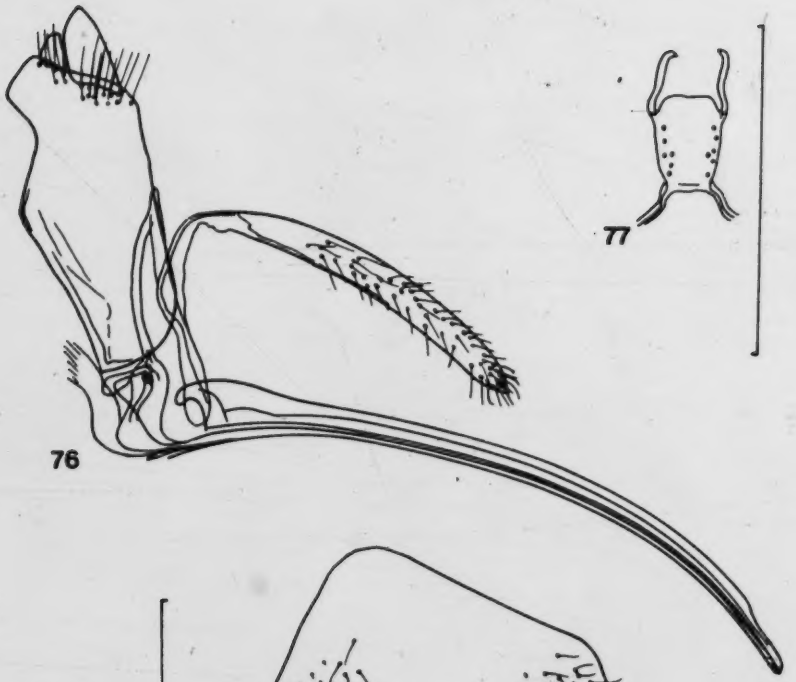
Figure 76. Female genitalia of *S. masoni*. In lateral aspect.

Figure 77. Oral plate of female *S. masoni*. In anterior aspect.

Figure 78. Hypopygium of *S. masoni*. In lateral aspect.

Figure 79. Male genital capsule of *S. masoni*. In dorsal aspect. Volsellae removed.

Figure 80. Male genital capsule of *S. masoni*. In lateral aspect. Volsellae except digitus removed.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Figures 81 to 88. S.E.M. photographs of *S. cinctiformis* female. Scale bars = 0.2mm.

Figure 81. Pronotum of *S. cinctiformis*. In lateral aspect.

Figure 82. Prescutellar furrow of *S. cinctiformis*. In dorsal aspect.

Figure 83. Scutellum of *S. cinctiformis*. In dorsolateral aspect.

Figure 84. Metapleuron of *S. cinctiformis*. In lateral aspect.

Figure 85. Metanotum and propodeum of *S. cinctiformis*. In dorsal aspect.

Figure 86. Anterior end of metasoma of *S. cinctiformis*. In dorsal aspect.

Figure 87. Hind coxa of *S. cinctiformis*. In lateral aspect.

Figure 88. Meso- and metasoma of *S. cinctiformis* male. In dorsal aspect.

85

Figures 89 to 93. Line drawings of *S. cinctiformis* female and male. Scale bars = 0.5mm.

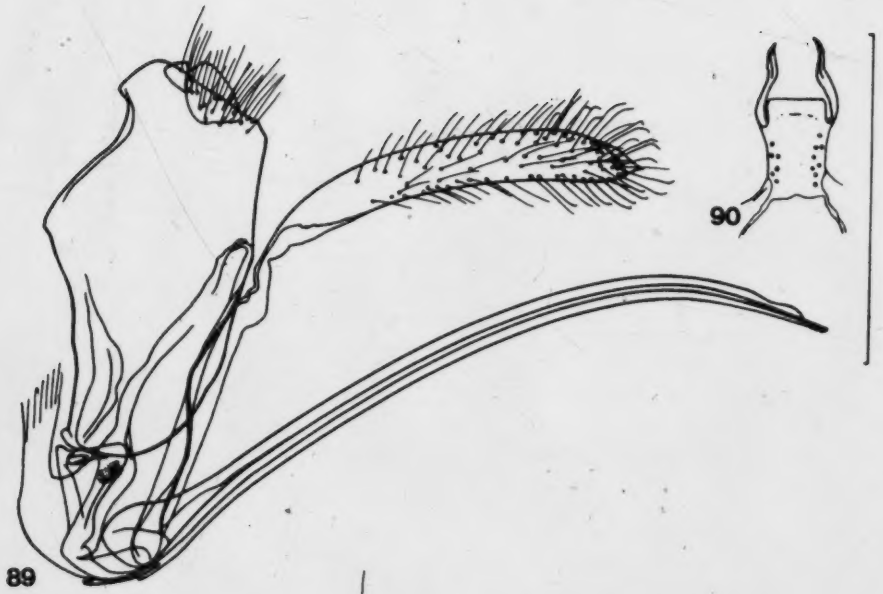
Figure 89. Female genitalia of *S. cinctiformis*. In lateral aspect.

Figure 90. Oral plate of female *S. cinctiformis*. In anterior aspect.

Figure 91. Hypopygium of *S. cinctiformis*. In lateral aspect.

Figure 92. Male genital capsule of *S. cinctiformis*. In dorsal aspect. Volsellae removed.

Figure 93. Male genital capsule of *S. cinctiformis*. In lateral aspect. Volsellae except digitus removed.



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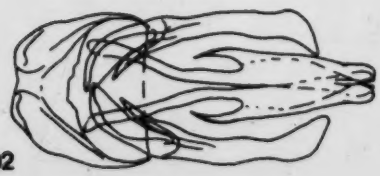

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Figures 94 to 101. S.E.M. photographs of *S. circumflexus* female. Scale bars = 0.2mm.

Figure 94. Pronotum of *S. circumflexus*. In lateral aspect.

Figure 95. Prescutellar furrow of *S. circumflexus*. In dorsal aspect.

Figure 96. Scutellum of *S. circumflexus*. In dorsolateral aspect.

Figure 97. Metapleuron of *S. circumflexus*. In lateral aspect.

Figure 98. Metanotum and propodeum of *S. circumflexus*. In dorsal aspect.

Figure 99. Anterior end of metasoma of *S. circumflexus*. In dorsal aspect.

Figure 100. Hind coxa of *S. circumflexus*. In lateral aspect.

Figure 101. Meso- and metasoma of *S. circumflexus* male. In dorsal aspect.

94
98
100

Figures 102 to 107. Line drawings of *S. circumflexus* female and male. Scale bars = 0.5mm.

Figure 102. Female genitalia of *S. circumflexus*. In lateral aspect.

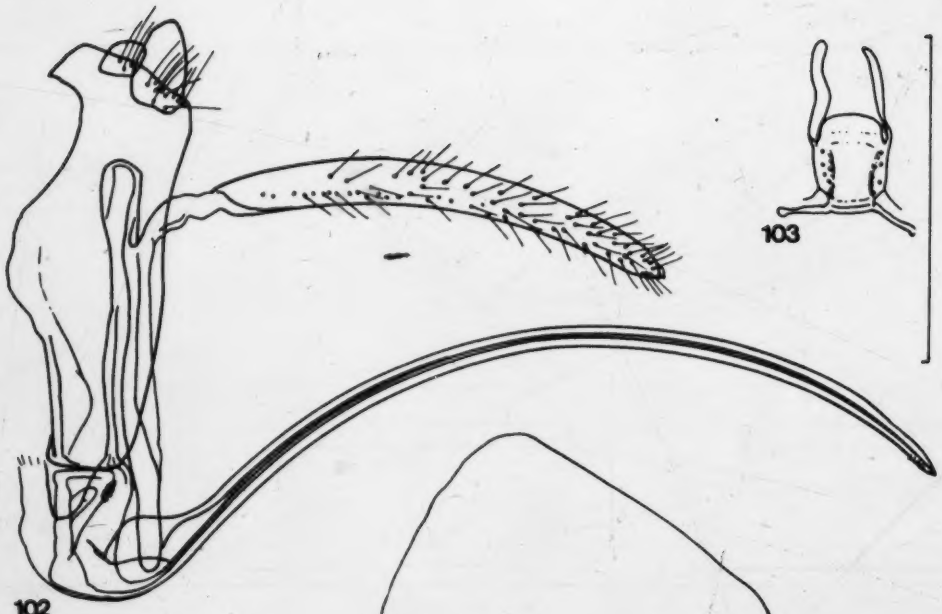
Figure 103. Oral plate of female *S. circumflexus*. In anterior aspect.

Figure 104. Hypopygium of *S. circumflexus*. In lateral aspect.

Figure 105. Head of adult *S. circumflexus*. In dorsal aspect.

Figure 106. Male genital capsule of *S. circumflexus*. In dorsal aspect. Volsellae removed.

Figure 107. Male genital capsule of *S. circumflexus*. In lateral aspect. Volsellae except digitus removed.



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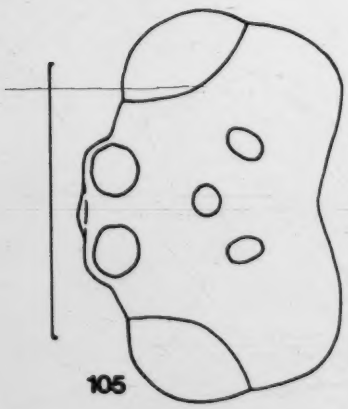

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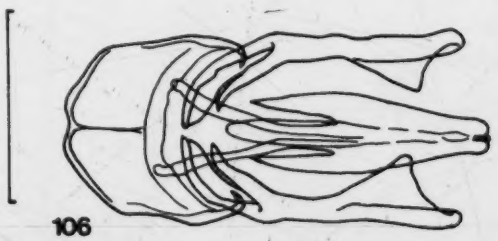

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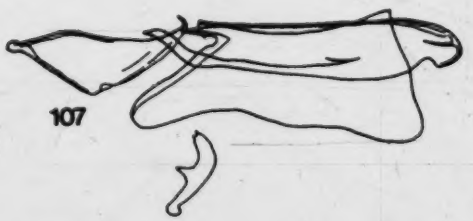


107

Figures 108 to 115. S.E.M. photographs of *S. neomexicanus* female. Scale bars = 0.2mm.

Figure 108. Pronotum of *S. neomexicanus*. In lateral aspect.

Figure 109. Prescutellar furrow of *S. neomexicanus*. In dorsal aspect.

Figure 110. Scutellum of *S. neomexicanus*. In dorsolateral aspect.

Figure 111. Metapleuron of *S. neomexicanus*. In lateral aspect.

Figure 112. Metanotum and propodeum of *S. neomexicanus*. In dorsal aspect.

Figure 113. Anterior end of metasoma of *S. neomexicanus*. In dorsal aspect.

Figure 114. Hind coxa of *S. neomexicanus*. In lateral aspect.

Figure 115. Meso- and metasoma of *S. neomexicanus* male. In dorsal aspect.

108
11
115

Figures 116 to 121. Line drawings of *S. neomexicanus* male and female. Scale bars = 0.5mm.

Figure 116. Female genitalia of *S. neomexicanus*. In lateral aspect.

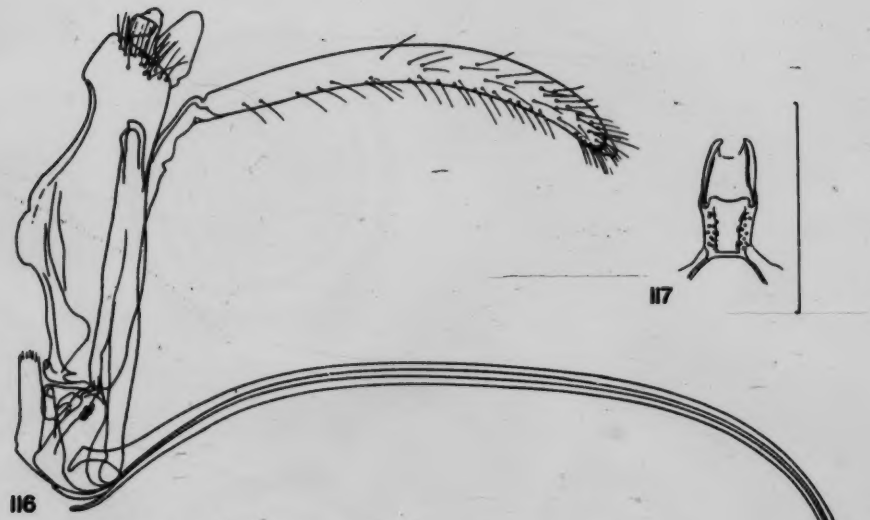
Figure 117. Oral plate of female *S. neomexicanus*. In anterior aspect.

Figure 118. Hypopygium of *S. neomexicanus*. In lateral aspect.

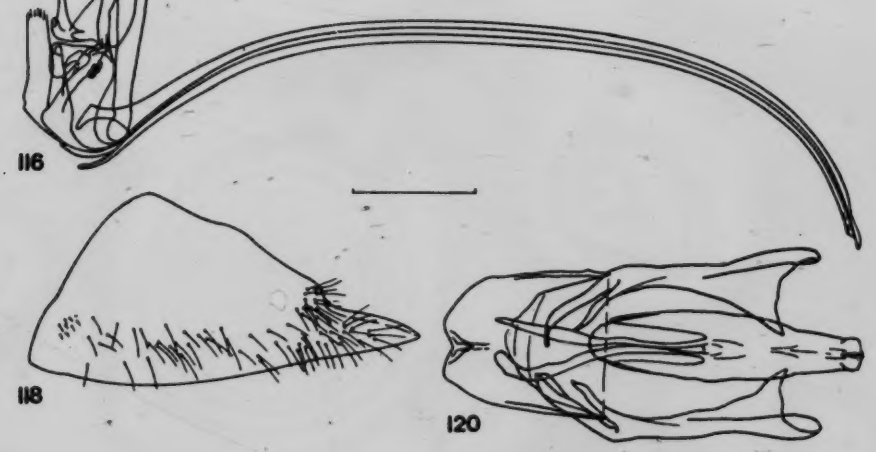
Figure 119. Head capsule of *S. neomexicanus* larva. In anterior aspect.

Figure 120. Male genital capsule of *S. neomexicanus*. In dorsal aspect. Volsellae removed.

Figure 121. Male genital capsule of *S. neomexicanus*. In lateral aspect. Volsellae except digitus removed.



117



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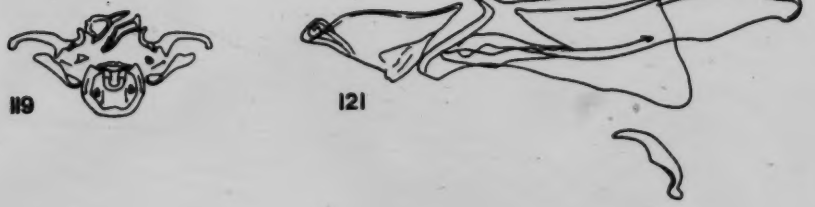

119

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Figures 122 to 129. S.E.M. photographs of *S. falcatus* female. Scale bars = 0.2mm.

Figure 122. Pronotum of *S. falcatus*. In lateral aspect.

Figure 123. Prescutellar furrow of *S. falcatus*. In dorsal aspect.

Figure 124. Scutellum of *S. falcatus*. In dorsolateral aspect.

Figure 125. Metapleuron of *S. falcatus*. In lateral aspect.

Figure 126. Metanotum and propodeum of *S. falcatus*. In dorsal aspect.

Figure 127. Anterior end of metasoma of *S. falcatus*. In dorsal aspect.

Figure 128. Hind coxa of *S. falcatus*. In lateral aspect.

Figure 129. Meso- and metasoma of *S. falcatus* male. In dorsal aspect.

124

Figures 130 to 136. Line-drawings of *S. falcatus* female and male. Scale bars = 0.5mm.

Figure 130. Female genitalia of *S. falcatus*. In lateral aspect.

Figure 131. Oral plate of female *S. falcatus*. In anterior aspect.

Figure 132. Hypopygium of *S. falcatus*. In lateral aspect.

Figure 133. Head capsule of *S. falcatus* larva. In anterior aspect.

Figure 134. Head of adult *S. falcatus*. In dorsal aspect.

Figure 135. Male genital capsule of *S. falcatus*. In dorsal aspect. Volsellae removed.

Figure 136. Male genital capsule of *S. falcatus*. In lateral aspect. Volsellae except digitus removed.

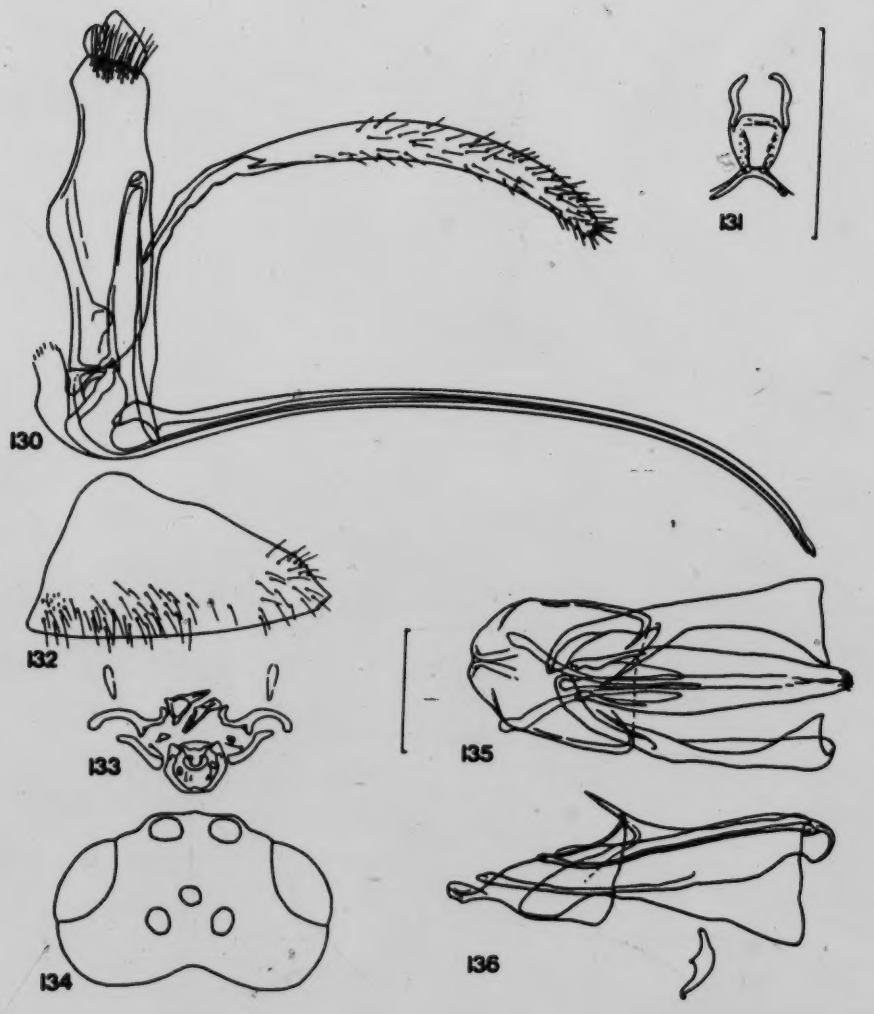
131
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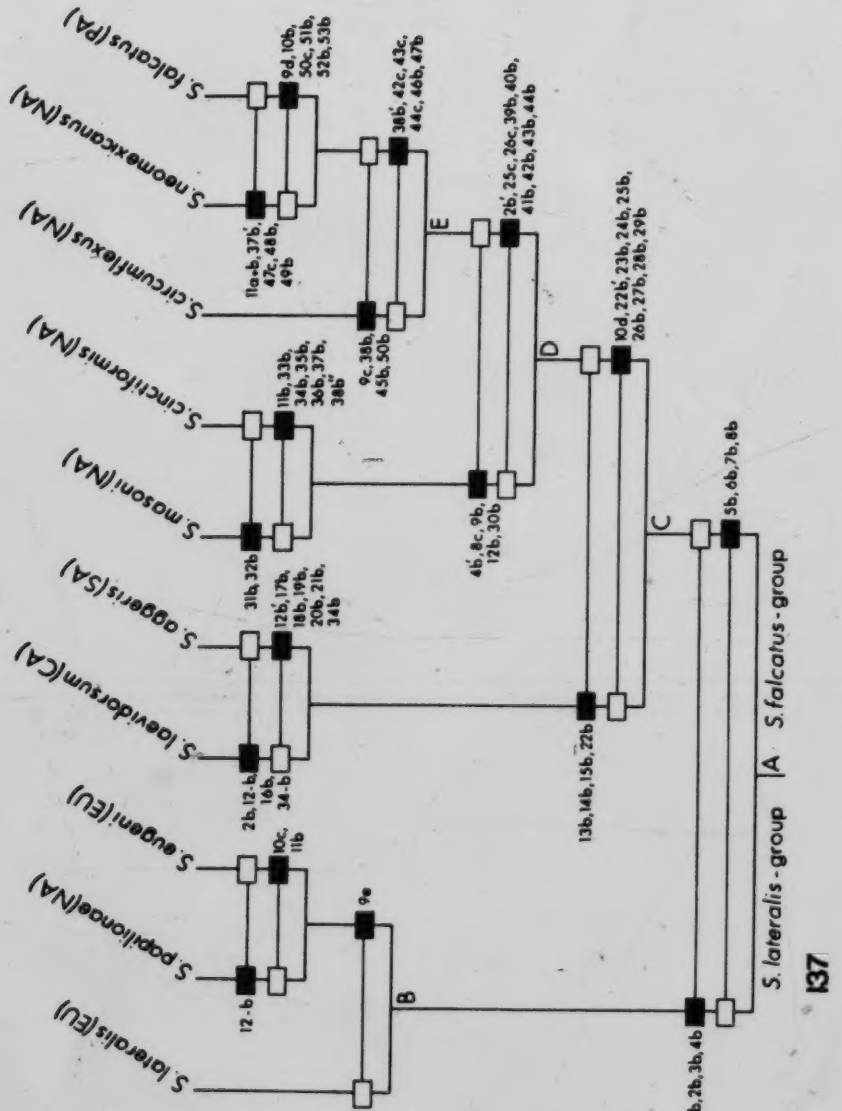
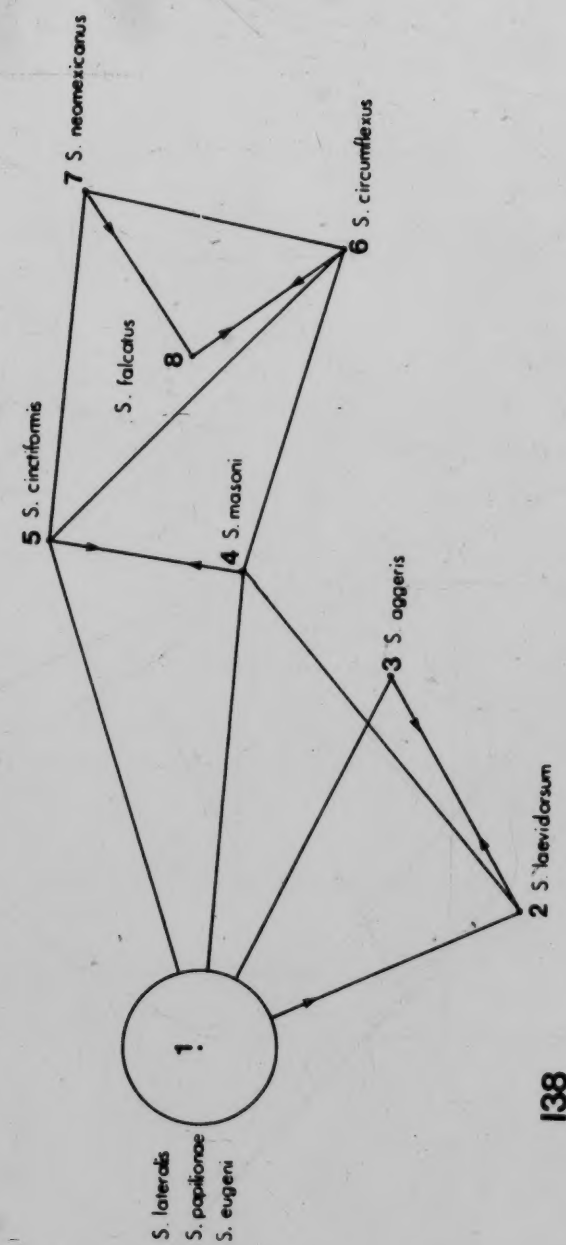
Figure 137. Reconstructed phylogeny of *Sathon* species. For explanation of characters and dichotomy coding see text (sect. 4). CA = Central America; EU = Europe; NA = North America PA = Palaearctic; SA = South America.


S. falcatus (PA)
S. neomexicanus (NA)
S. circumfloxus (NA)
S. cinctiformis (NA)
S. mosoni (NA)
S. aggeris (SA)
S. loeridorsum (CA)
S. eugeni (EU)
S. papilionae (NA)
S. lateralis (EU)
9d, 10b, 50c, 51b, 52b, 53b
11a-b, 37b, 47c, 48b, 49b
38b, 42c, 43c, 44c, 46b, 47b
9c, 38b, 45b, 50b
2b, 25c, 26c, 39b, 40b, 41b, 42b, 43b, 44b
4b, 8c, 9b, 12b, 30b
11b, 33b, 34b, 35b, 36b, 37b, 38b
31b, 32b
10d, 22b, 23b, 24b, 25b, 26b, 27b, 28b, 29b
13b, 14b, 15b, 22b
12b, 17b, 18b, 19b, 20b, 21b, 34b
2b, 12-b, 16b, 34-b
10c, 11b
12-b
9a
1b, 2b, 3b, 4b
3b, 6b, 7b, 8b
A
B
C
D
E
S. falcatus - group
S. lateralis - group

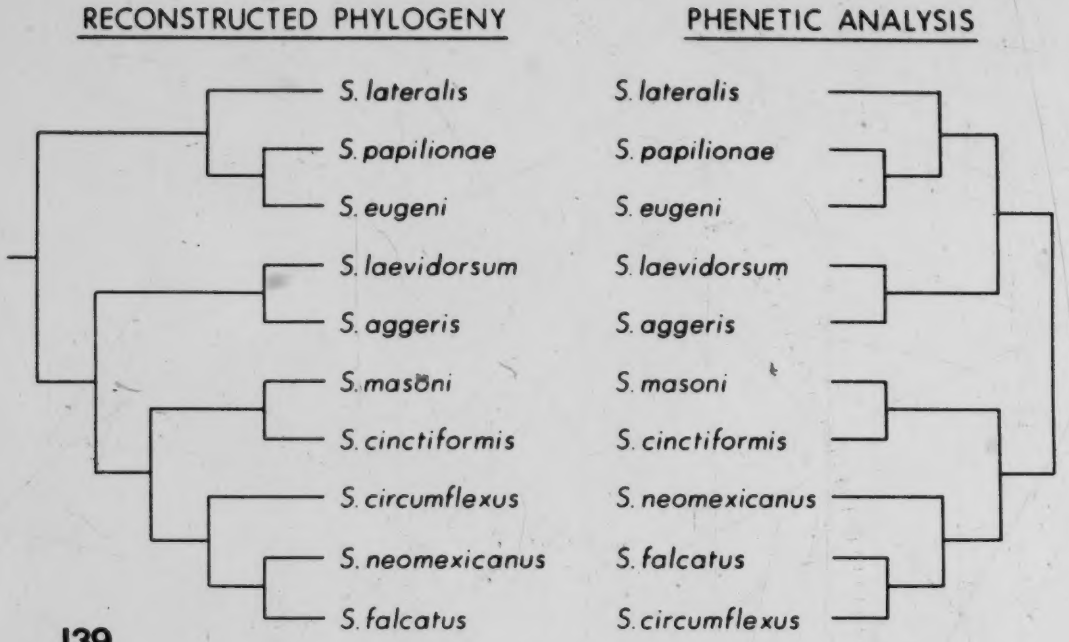
137

Figure 138. Cluster diagram of phenetic analysis of *Sathon* species. Each clusters nearest neighbor indicated by arrow on lines. The distance between *S. aggeris* and *S. masoni* is greater than indicated.


7 S. neomexicanus
6 S. circumflexus
S. falcatus
8
5 S. cinctiformis
4 S. masoni
3 S. aggeris
2 S. laevidorsum
1
S. lateralis
S. papilionae
S. eugeni

138

Figure 139. Comparison of phenetic and phylogenetic analyses. Degree of divergence not indicated.


RECONSTRUCTED PHYLOGENY
PHENETIC ANALYSIS
S. lateralis
S. papilionae
S. eugeni
S. laevidorsum
S. aggeris
S. masöni
S. cinctiformis
S. circumflexus
S. neomexicanus
S. falcatus
S. lateralis
S. papilionae
S. eugeni
S. laevidorsum
S. aggeris
S. masoni
S. cinctiformis
S. neomexicanus
S. falcatus
S. circumflexus

139

159

Figure 140. Distribution of *S. neomexicanus*. All dots represent localities from which *S. neomexicanus* specimens were examined in this study.

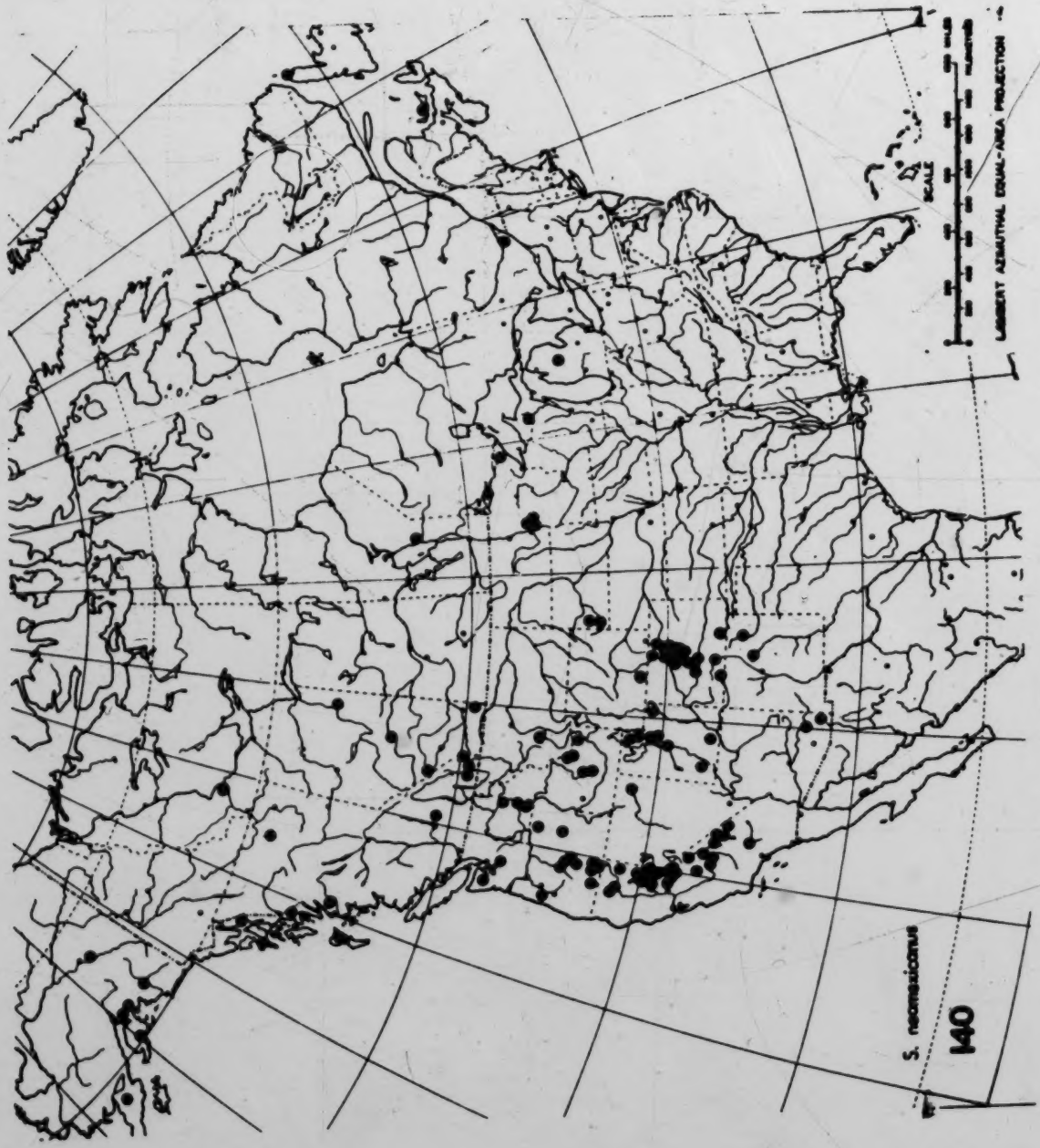
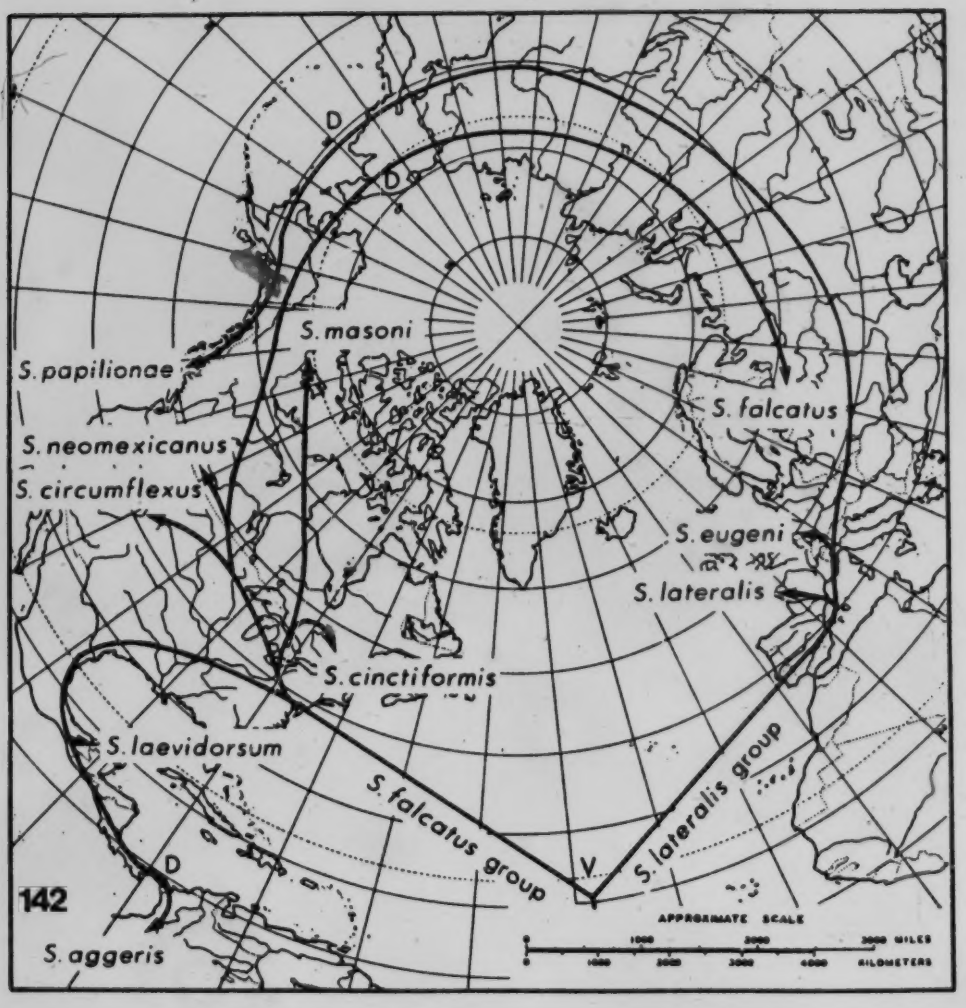

LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
S. neomexicanus
140

Figure 141. Distribution of American species of *Sathon* exclusive of *S. neomexicanus*. All dots represent localities from which specimens were examined in this study.

S. cinchiformis
S. circumflexus
S. masoni
S. papillonae
S. oggeri or S. laevidorsum
S. laevidorsum
S. oggeri
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

141

Figure 142. Geographical history of *Sathon* species, based on known distributions and reconstructed phylogenetic relationships. On polar projection. Arrows do not indicate direction of dispersal unless specifically indicated. D = probable dispersal route. V = probable vicariance event.


D
D
S. masoni
S. papilionae
S. falcatus
S. neomexicanus
S. circumflexus
S. eugeni
S. lateralis
S. cinctiformis
S. laevidorsum
S. falcatus group
S. lateralis group
V
D
142
S. aggeris
APPROXIMATE SCALE
1000
2000
3000 MILES
0
1000
2000
3000
4000 KILOMETERS

9. REFERENCES CITED

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. Kungliga Svenska Vetenskapsakademiens Handlingar 11:1-472.

Čapek, M. 1970. A new classification of the Braconidae (Hymenoptera) based on the cephalic structures of the final instar larva and biological evidence. The Canadian Entomologist 102: 846-875.

Carmichael, J.W. and P.H.A. Sneath. 1969. Taxometric maps. Systematic Zoolology 18(4): 402-415.

Carmichael, J.W., J.A. George and R.S. Julius. 1968. Finding natural clusters. Systematic Zoology 17(2): 144-150.

Claassen, P.W. 1921. *Typha* insects: their ecological relationships. Cornell University Agricultural Experiment Station Memoir 47: 459-531.

Cole, A.C. 1931. *Typha* insects and their parasites. Entomological News 42: 6-11, 35-39

Curtis, J. 1837. A guide to an arrangement of British insects; being a cataloge of all the named species hitherto discovered in Great Britain and Ireland. 294pp. London, published for the author.

Darlington, P.J. Jr. 1957. Zoogeography. 675pp. John Wiley and Sons, Inc. New York, London, Sydney.

Eady, R.D. 1974. The present state of nomenclature of wing venation in the Braconidae (Hymenoptera); its origins and comparison with related groups. Journal of Entomology (B) 43(1): 63-72.

Fahringer, J. 1938. Beiträge zur kenntnis der Braconidenfauna Chinas. Arkiv för Zoologi, Band

30A (12): 1-16.

Farris, J.S. 1979. The information content of the phylogenetic system. Systematic Zoology 28: 483-519.

Farris, J.S. 1982. Outgroups and parsimony. Systematic Zoology 31: 328-334.

Gautier, C. and H. Cleu. 1927. Hyménoptères Braconides: description d'une nouvelle espèce *d'Apanteles* parasite de *Hadena lateritia* Hfn. (Lep. Noctuidae). Annales de la Société Entomologique de France 96: 85-91.

Haliday, A.H. 1834. Essay on the classification of parasitic Hymenoptera. Entomologists Magazine 2(8): 225-259.

Hennig, W. 1966. Phylogenetic Systematics. 263pp. University of Illinois Press, Urbana.

Heppner, J.B. and G. Lamas. 1982. Acronyms for world museum collections of insects, with an emphasis on neotropical Lepidoptera. Bulletin of the Entomological Society of America 28(3): 305-315.

Hincks, W.D. 1944. A note on the nomenclature of some microgasterine Braconidae (Hym.). Entomologists Record and Journal of Variation 56: 19-20.

Hopkins, D.M. 1967. The Cenozoic history of Beringia - a synthesis. pp. 451-484. *In* Hopkins, D.M., ed., The Bering Land bridge. 495pp. Stanford University Press, Stanford.

Jakimavičius, A.B. 1972. New species of the genus *Apanteles* (Hymenoptera, Braconidae). Zoologicheskiĭ Zhurnal 51: 306-308.

MacPherson, A.H. 1965. The origin and diversity in mammals of the Canadian tundra. Systematic Zoology 14(3): 153-173.

Marsh, P.M. 1979. Braconidae. pp. 144-313. *In* Krombein, K.V., P.D. Hurd, D.R. Smith and

B.D. Burks, eds., Catalog of Hymenoptera in America north of Mexico. 2735pp. Smithsonian Institution Press.

Marshall, T.A. 1872. A catalogue of British Hymenoptera; Chrysididae, Ichneumonidae, Braconidae, ...Evaniidae *Oxytura*. London.

Mason, W.R.M. 1978. A synopsis of the nearctic Braconini, with revisions of *Coeloides* and *Myosoma* (Hymenoptera: Braconidae). The Canadian Entomologist 110: 721-768.

Mason. W.R.M. 1981. The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): a phylogeny and reclassification of the Microgastrinae. Memoirs of the Entomological Society of Canada 115: 147 pp.

Mayr, E. 1963. Populations, species, and evolution. 453pp. Belknap Press of Harvard University Press, Cambridge.

Mayr, E. 1969. Principles of Systematic Zoology. 428pp. Mcgraw-Hill Book Company, New York, St. Louis, San Francisco, Toronto, London, Sydney.

McKenna, M.C. 1972. Eocene final separation of the Eurasian and Greenland - North America landmass. 24th International Geological Congress 7:275-281.

Muesebeck, C.F.W. 1921 (1920). A revision of the North American ichneumon-flies belonging to the genus *Apanteles*. Proceedings of the United States National Museum 58: 483-576.

Muesebeck, C.F.W. 1922. A revision of the North American ichneumon-flies belonging to the subfamilies Neoneurinae and Microgastrinae. Proceedings of the United States National Museum 61(15): 1-15.

Muesebeck, C.F.W. 1958. Braconidae. pp. 18-36. *In* Krombein, K.V., ed., Hymenoptera of America north of Mexico. 305pp. USDA Agriculture Monograph 2. First supplement.

Muesebeck, C.F.W. 1967. Braconidae. pp. 25-51. *In* Krombein, K.V. and B.D. Burks, eds., Hymenoptera of America north of Mexico. 295pp. Supplement two. UDSA Agriculture Monograph 2.

Muesebeck, C.F.W. and L. M. Walkley 1951. Braconidae. pp. 90-184. *In* Muesebeck, C.F.W. and K.V. Krombein, eds., Hymenoptera of America north of Mexico. 1420pp. USDA Agriculture monograph 2.

Nees von Esenbeck, C.G. 1834. *Hymenoptorum Ichneumonibus affinum monographiae, genera europaea et species illustrantes*. 320pp. *Stuttgartiae et Tubingae*.

Nelson, G. 1973. Classification as an expression of phylogenetic relationships. Systematic Zoology 22: 344-359.

Nelson, G. and N.I. Platnick. 1981. Systematics and Biogeography, Cladistics and Vicariance. 567pp. Columbia University Press, New York.

Nixon, G.E.J. 1965. A reclassification of the tribe Microgasterini (Hymenoptera: Braconidae). Bulletin of the British Museum of Natural History. Entomology Supplement 2: 1-284.

Nixon, G.E.J. 1973. A revision of the north-western European species of the *vitripennis, pallipes, octonarius, triangulator, fraternus, formosus, parasitellae, metacarpellus* and *circumscriptus*-groups of *Apaneteles* Förster (Hymenoptera: Braconidae). Bulletin of Entomological Research 63:169-228.

Nelson, G. and N.I. Platnick. 1981. Systematics and Biogeography, Cladistics and Vicariance. 567pp. Columbia University Press, New York.

Paddock, F.B. 1933. Further notes on the Bee Moth. Journal of Economic Entomology 26: 177-181.

Pantin, C.F.A. 1969. Notes on microscopical technique for zoologists. 77pp. Cambridge University Press, Cambridge.

Papp, J. 1972. New *Apanteles* Först. species from Hungary (Hymenoptera: Braconidae: Microgasterinae), I. Annales Historico-Naturales Musei Nationalis Hungarici 64: 335-345.

Papp, J. 1983. A survey of the European species of *Apanteles* Först. (Hymenoptera: Braconidae: Microgastrinae), VIII. The *carbonarius-*, *circumscriptus-*, *fraternus-*, *pallipes-*, *parasitellae-*, *vitripennis-*, *liparidis-*, *octonarius-* and *thompsoni*-group. Annales Historico-Naturales Musei Nationalis Hungarici 75: 247-283.

Prance, G. (ed.). 1982. Biological diversification in the tropics. 714pp. Columbia University Press, New York.

Raven, P.H. and D.I. Axelrod. 1975. History of the flora and fauna of Latin America. American Scientist 63:420-429.

Rosen, D. 1975. The vicariance model of Caribbean Biogeography. Systematic Zoology 24:431-464.

Ross, H.H. 1945. Sawfly genitalia: terminology and study techniques. Entomological News 56: 261-268.

Shenefelt, R.D. 1972. Braconidae 4, Microgasterinae *Apanteles*. pp. 429-668. In *Hymenoptorum catalogus* (nov. ed.) Pars 7.

Simpson, G.G. 1951. The species concept. Evolution 5: 285-298.

Snodgrass, R.E. 1941. The male genitalia of Hymenoptera. 86pp. Smithsonian Institution Miscellaneous Collections 99(14).

Stevens, P.F. 1980. Evolutionary polarity of character states. Annual Review of Ecology and Systematics 11: 333-358.

Strickland, E.H. 1946. An annotated list of the Ichneumonoidea of Alberta. The Canadian Entomologist 77: 36-46

Talwani, M and G. Udintsev. 1977. Evolution of the Norwegian - Greenland Sea. Bulletin of the Geological Society of America 88: 969-999.

Thompson, J. W. 1972. Distribution patterns of American Arctic Lichens. Canadian Journal of Botany 50: 1135-1156.

Townes, H.K. 1969. Genera of Ichneumonidae part 1. Memoirs of the American Entomological Institute 11: 300pp.

Turekian, K.K. (ed.). 1971. Late Cenozoic Glacial Ages. 606pp. Yale University Press, New Haven, Connecticut.

Udvardy, M.D.F. 1969. Dynamic Zoogeography, with special reference to land animals. 445pp. Van Nostrand Reinhold Co., New York, Toronto.

Viereck, H.L. 1911. Descriptions of six new genera and twenty-six new species of ichneumon flies. Proceedings of the United States National Museum 40: 170-196.

Wiley, E.O. 1978. The evolutionary species concept reconsidered. Systematic Zoology 27: 17-26.

Wilkinson, D.S. 1937. A new species of *Apanteles* (Hym. Brac.) bred from *Myelois ceratoniae* attacking carobs in Cyprus. Bulletin of Entomological Research 28: 463-466.

Wilkinson, D.S. 1945. Descriptions of Palaearctic species of *Apanteles* (Hymen., Braconidae). Transactions of the Royal Entomological Society of London 95: 35-219.

Williams, D.J.M. 1985. The new world genus *Lathrapanteles* n. gen.: phylogeny and placement in the Microgastrinae (Hymenoptera: Braconidae: Cotesiini). Canadian Journal of Zoology 63: 1962-1981.

10. APPENDIX 1. TABLE OF RATIOS

Table 4. Non-coded, morphometric characters in *Sathon* species

For discussion of characters see text and see figs. 1 to 8 for measurement methods and structure abbreviations (abbreviations not given are PF = penultimate flagellomere and PFT = penultimate fore tarsomere). Columns are arranged with mean, range and standard deviation for each species. Sample sizes are listed after each species abbreviation. lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*.

Chars.	HW/HL	Clypeus W/H	pol/ool	pol/lol	lod/aod	lol/aod	PF W/L	PFT L/W	HW/HCL	SL/SW	2r/1Rs	1Rs+M/1M	1Cu1/m-cu
lat(6)	1.71	2.76	0.85	2.68	1.12	0.59	0.78	1.31	0.96	2.50	1.10	1.04	1.03
	1.54-1.88	2.55-2.91	0.76-0.94	2.50-3.00	1.05-1.22	0.56-0.67	0.67-0.90	1.13-1.50	0.88-1.04	-	1.00-1.30	1.02-1.10	0.96-1.08
	0.12	0.13	0.06	0.19	0.06	0.04	0.08	0.16	0.96	-	0.12	0.14	0.04
pap(2)	1.68	2.63	0.96	2.91	1.16	0.67	0.50	1.42	1.14	2.50	0.98	1.05	0.89
	1.63-1.73	2.50-2.73	0.76-1.13	2.57-3.25	1.13-1.18	0.47-0.86	-	1.33-1.50	1.13-1.15	-	0.96-1.00	1.02-1.08	0.88-0.90
	-	-	-	-	-	-	-	-	-	-	-	-	
eug(6)	1.82	2.91	0.74	2.37	1.10	0.64	0.62	1.41	0.99	2.50	1.04	1.04	0.92
	1.72-2.00	2.73-3.09	0.69-0.75	2.14-2.50	1.00-1.22	0.56-0.78	0.57-0.77	1.14-1.50	0.91-1.02	-	0.93-1.15	0.97-1.26	0.84-0.98
	0.11	0.13	0.06	0.17	0.07	0.08	0.09	0.13	0.06	-	0.08	0.11	0.05
lev(1)	1.67	3.00	0.65	2.60	1.14	0.71	0.67	1.33	1.00	2.60	1.16	1.05	1.00
	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	

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Table 4 (cont.). Non-coded, morphometric characters in *Sathon* species

Char.	HW/HL	Clypeus W/H	pol/ool	pol/lol	lod/aod	lol/aod	PF W/L	PFT L/W	HW/HCL	SL/ SW	2r/1Rs	1Rs+M/ 1M	1Cu1/ m-cu
agg(1)	1.70	3.90	0.69	2.67	1.13	0.75	0.66	1.83	0.90	3.00	1.83	0.93	1.00
	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	
mas(16)	1.72	2.95	0.81	2.13	1.10	1.10	0.87	1.28	1.21	2.50	0.77	0.97	0.96
	1.62-1.81	2.67-3.33	0.62-0.95	1.75-2.43	1.00-1.25	0.93-1.33	0.78-1.00	1.17-1.33	1.10-1.49	-	0.58-0.91	0.92-1.04	0.83-1.10
	0.05	0.22	0.09	0.19	0.10	0.12	0.08	0.08	0.09	-	0.08	0.03	0.07
cin(15)	1.68	3.04	0.78	2.25	1.15	0.84	0.69	1.10	1.13	2.80	0.77	0.96	0.96
	1.57-1.78	2.80-3.30	0.67-0.89	1.89-2.67	1.00-1.43	0.67-1.00	0.62-0.82	1.00-1.28	0.99-1.53	-	0.57-0.95	0.92-1.00	0.74-1.11
	0.07	0.17	0.06	0.23	0.11	0.11	0.06	0.10	0.12	-	0.10	0.02	0.10
cir(15)	1.83	3.00	0.93	2.40	0.97	0.79	0.67	1.23	1.17	2.00	1.03	1.10	1.16
	1.67-1.98	2.58-3.33	0.80-1.00	2.00-2.83	0.89-1.05	0.67-0.89	1.14-1.38	1.10-1.26	-	0.87-1.24	1.06-1.17	0.95-1.39	
						0.57-0.75							
	0.07	0.19	0.06	0.21	0.06	0.08	0.05	0.09	0.05	-	0.09	0.03	0.10
neo(35)	1.87	3.00	0.92	2.22	1.07	0.84	0.63	1.23	1.11	2.40	0.85	1.06	1.00
	1.66-2.08	2.54-3.50	0.81-1.05	1.88-2.67	0.91-1.25	0.60-1.00	0.53-0.69	1.00-1.43	0.97-1.28	-	0.57-1.18	0.98-1.13	0.82-1.15
	0.09	0.24	0.07	0.17	0.07	0.10	0.04	0.18	0.06	-	0.10	0.04	0.11
fal(25)	1.89	3.06	0.99	2.27	1.14	0.83	0.79	1.06	1.06	2.50	0.98	1.12	1.13
	1.75-2.03	2.75-3.30	0.88-1.12	2.11-2.50	1.00-1.33	0.73-0.90	0.69-0.91	1.00-1.13	1.00-1.14	-	0.78-1.13	1.02-1.19	0.88-1.35
	0.07	0.13	0.06	0.13	0.07	0.06	0.06	0.06	0.03	-	0.09	0.04	0.10

11. APPENDIX 2. LOCALITY DATA

MATERIAL EXAMINED FOR PREVIOUSLY DESCRIBED SPECIES.

(Type material not included)

11.1 *S. eugeni*

Germany: Female, Germany '65 Mainz Sept. 10 A.W. Steffan (CNC). **Italy**: Female, Campi, Riva s. Garda 1400m. E/7.7.66 Hbth (LAZ). **Holland**: Female, Nederlands Oostbroek im Den Bilt coll. 25.V.1979 R. v. Oostenbragge. ex leafroller on Urtica dioica d. (RNH). **Sweden**: Female, Skåne, Sweden VII '69 Trap 4 Bo Svensson (HT). Female, Sweden Vmld. Ekshärad July 23 1960 W.R.M. Mason (CNC). 2 females, Sweden. Sk. Skäralid 3.vii.1938 D.M.S.P. & J.F.P., B.M. 1938-414 (BMNH). **Bulgaria**: 2 females, BULGARIA Rhodopi Chrabrino 15.V.1978, 9.X.1977 (DJMW).

11.2 *S. lateralis*

England: 2 males, 2 females, Torquay, Devon ENGLAND 19-vi-1960 J.R. Vockeroth (CNC). Male, female, ENGLAND East Sussex Staplecross 15-19.ix.38 RF 139. D.S. Wilkinson & R.L.E. Ford. Swept off nettle where Simaethis fabriciana abundant (BMNH). **Germany**: Female, Gessernhausen Brennessel leg. Schwenke 14./E.5.69 Z.59 (LAZ). **Irelend**: 6 males, 4 females, Finglas, Ireland vi.44 B.P. Beirne Ex Simaethis fabriciana (CNC). 2 females, Ballybrack, Ire vi.41 B.P. Beirne Ex Simaethis fabricians (CNC). **Holland**: Male, NEDERLAND Waarder (Z.H.) Oosteinde 34 2-3.X.1971 C van Achterberg. Alnus-Salix-forest. on peat in cult. area, Townes-trap (RNH). Male, NEDERLAND Waarder (Z.H.) Oosteinde 1-5.VII.1971 C. van Achterberg (RNH). Male, 5 females, NEDERLAND (Z.H.) Waarder: at 0.33 in Malaise Trap 16-31 Sept. 1973 (DJMW). Male, female, Nederlands, Oostbroek 1250 im. Den Bilt. coll. 1.VI.1979 R.v. Oostenbragge. ex leafroller on

Urtica dioica d. (RNH).

11.3 *S. cinctiformis*

Canada. Ontario: 2 males, female, Ottawa, Ont. 19-VII-1939, 28-VI-1940, O. Peck (CNC). Female, Ottawa Can P310 Type Apanteles cinctus Prov. (USNM). Female, Ottawa, Ont. 9-VII 1946 G.S. Walley Dow's Swamp (CNC). Female, Ottawa, Ont. 21-VII 1950 W.R.M. Mason (CNC). **Quebec**: 2 females, Gracefield, Que. 15-VI.1937 O. Peck (CNC). Female, Wakefield, Que. 9.VII 1946 G.E. Shewell (CNC). Male, Brome, Que. 12-VI 1936 G.S. Walley (CNC). **United States. Indiana**: 2 male, female, Lafayette Ind May 1918 JM Aldrich coll (USNM). **Iowa**: 2 male, 2 female, County #76 IOWA May 26 1934 Knutson (USNM). Male, County #59 IOWA May 1934 Jolley (USNM). Female, Mt Pleasant Ia May 26 1934 Card (USNM). **Maryland**: Female, Takoma Park, VI.14, 1942 Md. H. & M. Townes (HT). Female, Cabin John Md. July 1916 RM Fouts Collector (USNM). Female, Patuxent Ref Bowie, Md. 28-V 1944 RT Mitchell Collector (CNC). **Michigan**: 2 male, female, Isabella Co. Mich. 6-7-58 R. & K. Dreisbach (USNM). Female, Gladwin Co. Mich. 6-14-58 R. & K. Dreisbach (USNM). Female, Lake Co. Mich. 7-7-57 R. & K. Dreisbach (USNM). 4 females, Midland Co. Mich. VI.10.41, VII.7.54, 7-18-40, 6-30-52, R.R. Dreisbach (USNM). Female, Ag. Coll. Mich 7-12.9-336 Collection C.F. Baker (USNM). Female, AgrCollege Mich 336 (USNM). **New Jersey**: Female, Summit N.J. 5.26 1925 F.M. Schott (USNM). **New York**: Male, Oswego, N.Y. 11 June, 1897 (USNM). Male, female, Mud Creek, Tompk Co. N.Y. 17-20 June '04 (USNM). 2 male, female, Ithaca, N.Y. V.31, 1936, VI.6, 1935, H.K. Townes (HT).Female, Bemus Pt., N.Y. Jul. 16 1937 H.K. Townes (HT). Female, Oneoata NY June 30 1935 H.K. Townes (HT). Female, Shokan, N.Y. Jul. 11 1936 H.K. Townes (HT). Female, Canajoharie, N.Y. Jul. 1, 1934 H.K. Townes (HT). **North Carolina**: Female, Franklin, N.C. 2000' 8.11 1957 J.R. Vockeroth (CNC). **Ohio**: 3 females, Barberton Ohio 6-22-36 L.J. Lipovsky (UKL). 2 females, Summit Co., Ohio 6-19 1937 Louis J. Lipovsky (UKL). Female, Conservation Cage

Jerusalem Ohio In3 Ser33-1 LG Jones Coll 6/10/33 (USNM). Female, Ohio F.D. DeGant Collector (USNM). Female, Lick. Co. V-'26 O. C.H. Kennedy Collector, C.H. Kennedy Collection (USNM). **Pennsylvania**: Female, Wilawana, Pa. 6-9 1939 R.H. Crandall (USNM). Female, Ralston Lycoming Co. Pa. 8.VI.1962 J.R. Vockeroth (CNC). **Rhode Island**: Male, 8 females, Westerly, R.I. VI.9, VI.10, VI.21, VII.7, 1936 M. Chapman (HT). Female, Westerly R.I. VI.12.37 H.K. Townes M. Chapman (HT). **Vermont**: Female, Lake Willoughby, Vt. Alt. 1400ft. June 17-29, 1945 C.P. Alexander (HT). **Virginia**: 3 males, 3 females, Sweeping sedges & grasses Vienna Va J.C. Bridwell coll V-19-35 (USNM).Female, Va July 4.85 (USNM). Female, Great Falls Va H.H. Smith coll (USNM). Female, Ch. Bridge XI.19 Va SA Rohwer coll (USNM). **Wisconsin**: Female, Polk Co. Wis. July. Baker. Collection CF Baker (USNM).

11.4 *S. falcatus*

Austria: Male, 14 females, AUSTRIA Tirol Aschbach 1400m 16, 20-VIII 1975 C.J. Zwakhals (RNH). 2 females, AUSTRIA, Raxalpe 1500m Aug.20, 1960 W.R.M. Mason (CNC). Female, Zwieselstein TIROL 1400m. 24.VIII.1953 J.R. Vockeroth (CNC). **England**: Female, ENGLAND. HT. Bricket Wood. 5.v.1950 R.B. Benson B.M. 1950-286 (BMNH). Male, 5 females, ENGLAND North Devon Romansleigh R.L.E. Ford Swept 26.vi.38 (CNC, USNM). 5 females, Ditchling Common 1.VIII.1951. Sx. G.E. Shewell ENGLAND (CNC). 5 males, 3 females, ENGLAND Birmingham spun 16.vii.55 em. 20.vii.55 [with two cocoon masses] (BMNH). **France**: Male, 2 females, Malaucène Mt. Ventoux 1400m. Nardion pasture 23.VII.1973 FRANCE Dept. Vaucluse M.J. Gijswijt (RNH). **Germany**: 5 females, Scheffau, Bayern GERMANY, 800m. 25-VII-1958 David Townes (CNC). Female, D, By, Starnberg Kerschlach 27.7.74 Haeselb. (LAZ). Female, Wiesen/Spessart 6.8.1961 leg. Haeselbarth (LAZ). 3 females, Schliersee BAVARIA 7-1100m. 28.VII.1958 David Townes (CNC). 2 females, Germany Collection T Pergande 26 (USNM). **Holland**: Female, Holland 28-7-49 Schayk H. Teunissen (RNH). Female, Oploo HT V-5 1972 (RNH). 3 females, NEDERLAND

Waarder (Z.H.) Oosteinde 34 3-4, 13-14, 27-28.VII.1971 C. van Achterberg (RNH). **Italy**: 8 males, 20 females, Naturno, Trentino ITALY 500-1000m., 1000m., 14-VII, 15-VII, 18-VII.1958 David Townes (CNC). Female, Unserfrau, 1500m nr. Mont Alto, Trentino, ITALY 18-VII-1958 David Townes (CNC). Male, St. Peter/Ahrntal [=San Pietro], Südtirol 1300m. Cd/31.7.66 Haeselbarth (LAZ). Female, S. Pietre 1200-1400m Funes-[Villnö] prov. Bolzano-Italia 20.vii-9.viii.1968 G. van Rossem (RNH). Female, Selva Nera 1400-2000m Funes-[Villnö] prov. Bolzano-Italia 20.vii-9.viii.1968 G. van Rossem (RNH). **Ireland**: Female, M-IRELAND nr. Rhode (3) Heath, on umbelliferous flowers 11-VIII. 1974 C.v. Achterberg (RNH). **Luxemburg**: Female, LUXEMBURG Diekirch, 20-V/A.W. Steffan '66 (CNC). **Spain**: Female, LA MOLINA 1500m 23-VII-1970 ESPANIA Gerona V.S.v.d. Goot J.A.W. Lucas (RNH). **Sweden**: 20 males, 60 females, SWEDEN, Vmld. Ekshärad July 15, 17, 20, 21, 22, 23, 24, 1960 W.R.M. Mason (CNC). Male, 7 females, SWEDEN, Lpld. Abisko, 400m. July 2, 30, Aug 1, 2, 30, 1960 W.R.M. Mason (CNC). **Switzerland**: Female, CH, GR, Ramosch 165om 4.8.73 Wiesen u.Wald mit Hochstauden Haeselb. (LAZ). **Yugoslavia**: Female, Yougoslavia, Slovenia Swept:16-8-1978 leg. H.V. Vlug stol. 1000m (RNH). **Other**: 6 females, no locality data, 2 det. by O. Schmiedeknecht (USNM).

11.5 *S. neomexicanus*

Canada. Alberta: 5 males, 3 females, Canada Alberta, Livingstone Ranger Stn. 49° 50'N 114° 25'W Malaise, Sweeps 9-31 July, 20 August 1980 D.J. Williams (DJMW, LAZ). Male, 4 females, M. 14 Banff Banff-Jasper Hway 2,3-VIII-1955 R. Coyles (CNC, BMNH). Male, female, McMurray, Alta. 30-VIII-53 G.E. Ball (CNC). Female, Elkwater Lk. Alta. 21-VII-1956 O. Peck (CNC). Female, O. Peck Edmonton, Alta. 13-5-1930 (CNC). Female, Dom. Range Sta. Manyberries, Alta 24.VII.1951 D.F. Hardwick (CNC). **British Columbia**: 3 males, Racing Riv., B.C. 2400ft. VII.25.73 H.&M. Townes (HT). 4 females, Shore, Shuswap L Salmon Arm B.C. 13-VII-49 H.B. Leech Collector (CAS). 3 females, Juskatla, B.C. Q.C.

[Queen Charlotte] Islands 9-VIII-1957 E.E. MacDougall (CNC). Female, Lizard Cr. Fernie B.C. 7-VII-1949 Hugh B. Leech (CAS). Female, Kaslo BC 16.9 [or 7?] AN Caudell Collector (USNM). Female, Terrace, B.C. 23.VII-1960 W.R. Richards (CNC). **Prince Edward Island**: Male, Dalvay House Can. Nat. Park P.E.I. 20.Viii-1940 G.S. Walley (CNC). **Northwest Territories**: 3 females, Fort Simpson N.W.T. 15, 17, 19.VIII.1950 D.P. Whillans (CNC). **Newfoundland**: 3 females, Calvert Nfld. 16-VII-1958 Ray F. Morris (CNC) 3 males, 5 females, Goose Bay, Labr. 5, 10, 23, 25, 26.VIII.1948 W.E. Beckel (CNC). Female, Raleigh, Nfld. VIII.4.1975 H.&M. Townes (HT). **Ontario**: Female, Bells Corners Ont. 7-VII 1943 G.S. Walley (CNC). Female, One Sided Lake, ONT. July 31-1960 S.M. Clark (CNC). **Manitoba**: Male, 2 females, Berens River, Man 9-vii-1938 W.J. Brown (CNC). **United States. Alaska**: Female, King Salmon, Naknek R. Alaska 8-VIII-1952 J.B. Hartley (CNC). Female, Seward, Alaska 10-VII-1951 W.J. Brown (CNC). Male, ALASKA: Sitka 0-100m. VII-1970 Collected by N.L.H. Krauss (USNM). Female, Junaeu, Alaska 6 VIII 1958 Wot Coll. (HT). Male, Matanuska Alaska VII-18-44 J Chamberlin 44-27645 Trap (USNM). Female, Chitna Alaska 7 Aug 1956 R.H. Washburn (USNM). Female, Wrangell, ALASKA 1-5.VIII.1951 J.R. McGilllis (CNC). Female, Big Delta Alaska 14.VII 1951 J.R. McGillis (CNC). Female, Eagle Riv., SE Alaska 2 VIII 1958 Wot Coll. (HT). **Arizona**: 2 females, ARIZ. Graham Co. Hospital Flat Pinaleno Mts. Alt. 8950' 2.VIII.1965 Hugh B. Leech (CAS). Female, ARIZONA: Cochise Co. Southwestern Res. Sta., 5mi W. Portal 24-IX-1966 5400' P.H. Arnaud, Jr. (CAS). **California**: Female, Graeagle Calif. VI.16 1949 E. Schlinger (HT). Female, Lee Vining, Cal. June 22 1948 HMG&D Townes (HT). Male, 3 females, Sagehen Creek Nevada Co., Cal. VII.10.1974 R.M. Bohart (HT). 7 males, 5 females, Sagehen Creek nr. Hobart Mills Nevada Co. Cal. VII-8, 15-1964 (UCD). Female, Sagehen Cr. Nevada Co Calif VII-19 1972 RM Bohart Colr (UCD). Male, 3 females, Sagehen nr. Hobart Mills Calif VII-21-58 R.H. Goodwin Collector (USNM, UCB). 5 males, 3 females, Sagehen Cr., nr Hobart Mills, Nevada Co, Cal. VII-15, 16, 19-64; ME Irwin Malaise in meadow (USNM). 4 males, 2 females, CALIF: Sierra Co. Sagehen Creek Field Station VIII-6-75 M.E. Buegler/E.I. Schlinger (UCB). 4 females, Cal Nevada Co

Sagehen Ck nr. Hobart Mills VII-8-1974 Wharton, Coll (BWC). 3 males, 6 females, Prosser Creek, near Hobart Mills, CALIF. 6300' 13.VII.1961 B.H. Poole (CNC). Male, female, CA: Placer Co. old Donner Pass 2 mi E. Norden 9-IX-1983 7000' J.B. Whitfield collector (JWC). Female, Cal Alpine Co 2mi E. Monitor Pass VII-8-74 Wharton Coll (BWC). 3 females, CALIF: Sisk. Co. 1mi NW Bartle, VII-20-66 P. Rude collector (UCB). 4 males, 4 females, McBride Springs, 4800' Mt. Shasta, Siskiyou Co. Calif., July 22, 1965 (CNC). Female, Cedar Pass, 6000' Warner Mts. 8.VIII.65 Modoc Co., Calif. (CNC). 4 males, 3 females, Fish Camp Cal. July 15 1948 HMG&D Townes (USNM). Female, Walker Pass Cal. VII-13-61 E.I. Schlinger Collector (USNM). Female, Mammoth Lake Calif. VII-29-1940 D.E. Hardy (UKL). Female, Bishop, Calif. VII-28-40 R.H. Beamen (UKL). 2 males, Yosemite Nat. Pk. Calif VIII-1 1940 D.E. Hardy (UKL). 2 males, 2 females, Fallen Leaf, Calif. Eldorado Co. 13.VIII.1961 6500' B.H. Poole (CNC). 3 males, 9 females, Truckee, CALIF. 6000' Tahoe Co. 14.VIII.1961 B.H. Poole (CNC). 2 females, Shaver Lake Fresno Co. Calif VII-8,13-56,68 J.B. Hay flight trap, R.O. Schuster Collector (UCB). Male, Hope Valley Alpine Co. Calif VII-18-48 D. Carter Collector (UCB). Male, female, Lake Forest Lake Tahoe Calif. VII.23.49 E.G. Linsley Collector (UCB, USNM). Female, Leland Mdw. Tuolumne Co. Calif. VIII-5-60 E. Jensen Collector (UCB). Male, Leavitt Mdw. Mono Co., Calif. VIII-11-60 E. Jensen Collector (UCB). Female, Cisco Cal Placer Co VII.28 1934 J.C. Downey collector (UCD). Male, 4mi. W Woodfords Cal. Alpine Co. VI-25-1961 A.S. Menke collector (UCD). Female, Smith Mill Cal. 15 mi s.e. Sierraville VII-4-1960 F.D. Parker Collector (UCD). Female, Wawona, Cal. VII-12-48 H.K. Townes (USNM). Female, Lake Tahoe, Cal. Alt 6225ft. VII-24-1949 E.G. Linsley Collector (UCB). **Colorado**: 3 males, 7 females, Loveland Pass W. slope 9850' 28.VII, 8.VIII.1961 COLO. B.H. Poole (CNC). Female, Alamosa Colo. 1963 D.E. Hahn (HT). Male, 2 females, Morley, Colorado Aug. 25, 1940 H.&M. Townes (HT). 3 males, 3 females, Gould, Colo. VIII.6, 7.1974 H.&M. Townes (HT). Female, nr. Estes Pk. Colo. VIII.14.1948 HMG&D Townes (HT). 5 males, 1Females, Estes Park, COLO. 7500' 20-VII-61 J.R. Stainer, S.M. Clark, W.R.M. Mason (CNC). 4 males, 18 females, Doolittle Ranch 9800'

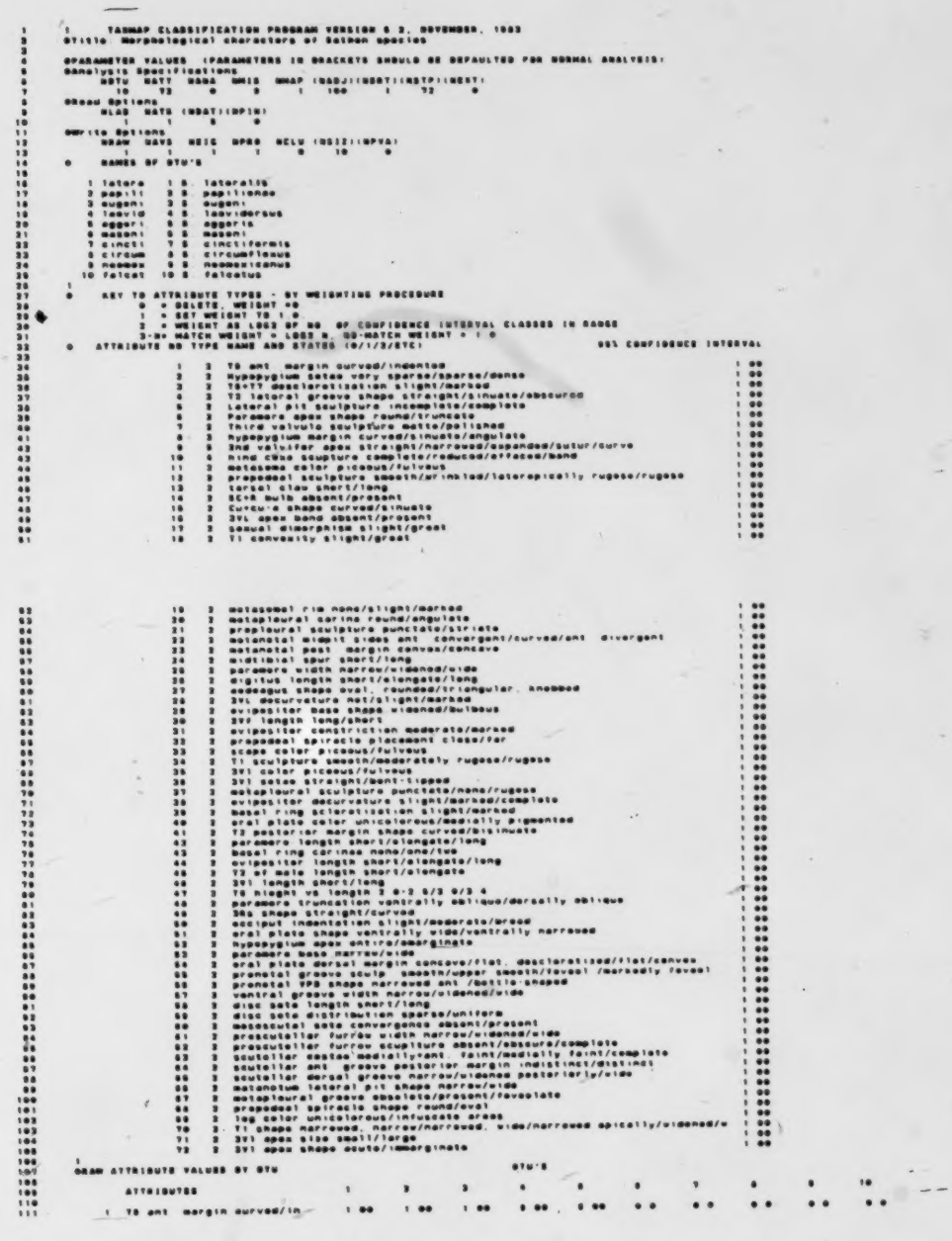
Mt. Evans COLO. 17, 23, 31-VII and 3, 8, 9, 10, 12, 13-VIII '61 J.R. Stainer, S.M. Clark, B.H. Poole, W.R.M. Mason (CNC). Female, West Chicago Creek, Idaho Springs Colo., 11.VIII.1961 9800' J.E.R. Stainer (CNC). 6 females, West Chicago Cr. 9800' Clear Cr. Co., COLO. 11-VIII-1961 B.H.Poole, S.M. Clark (CNC). 3 males, 4 females, Chicago Cr. 8800' Clear Cr. Co. COLO. Aug 2,5 1961 B.H. Poole, W.R.M. Mason (CNC). Female, Glen Haven Colo. VIII.3.1947 P.B.&E.R. Lawson (UKL). 2 females, USA: Colorado: Teller County, Florrisant, Petrified Forest Area 2530m 11-VIII-1973 Paul H. Arnaud, Jr. (CAS). Male, 2 females, State Bridge 7000' nr. Bond, COLO. 24-25-VI-61 B.H. Poole, C.H. Mann (CNC). 2 males, female, Fairplay, COLO. 9800'15 July '61 S.M. Clark, W.R.M. Mason (CNC). 2 males, 19 females, Mt. Vernon Cn. nr. Golden COLO. 31-VII-61 7200'C.H. Mann, W.R.M. Mason (CNC). 6 males, 10 females, 4mi. S.W. Golden, Colo. 7400' 31-VII-1961 S.M. Clark (CNC). Female, Jefferson, COLO. 9400' 14-VII-61 S.M. Clark (CNC). Female, Boulder Colo. 8.VIII 1961 C.H. Mann 5300' (CNC). Male, Nederland, COLO. 8200' 29-VI-61 Collector W.R.M. Mason (CNC). Female, Nederland, Colo. 3mi N. 8500' J.G. Chillcott (CNC). Male, Wondervu, Colo. Boulder Co. 8800' 11.VIII.1961 J.G. Chillcott (CNC). Male, Fall R. RMNP Colo. 8600ft Aug 18 48 Evans & Ball (CNC). 3 females, Idaho Springs, 5mi S.W. Colo. 27.VIII.1961 8000', 8600' C.H. Mann (CNC). Female, Gothic, Colo 9600ft 7-1929 Mary J. Brown (USNM). Male, Boulder Canyon Colo. 8-8-60 7800' R.,K. Dreisbach (USNM). Female, Pagosa Springs Col. Baker Collection CF Baker (USNM). Female, Poudre L. Col. RMNP 1100ft. Aug. 11, 1948 HMG&D Townes (USNM). 10 males, 13 females, Colo 1329 [Steamboat Springs, July], 1361 [Foothills w. of Fort Collins, June], 1547 [Fort Collins. 6-7-95], 1583 [Rustic. 7-11-95], 1584 [Fort Collins. 8-1-95], 2009 [Mooris Ranch, Lar. Co. 7-19-96], 2013 [Forresters Ranch. 8-3-96], 2024 [Spicers North Park. 7-18-96], 2044 [Fort Collins. 7-10-96], 2158 [Grizzley Peak. 7-24-96] Collection CF Baker (USNM). **Idaho**: Male, 3 females, 2 1/2 mi N.W. Kilgore, Clark Co., Ida. VII-15-1956 W.F. Barr Collector (USNM). Female, 2mi N Gilmore, Ida. Lemhi Co. VII-24 1959 H.C. Manis Colector (USNM). Male, 2 mi. E. Leadore Lemhi Co. Ida. VII-12-1956 W.F. Barr Collector (USNM). 2 females, Galena

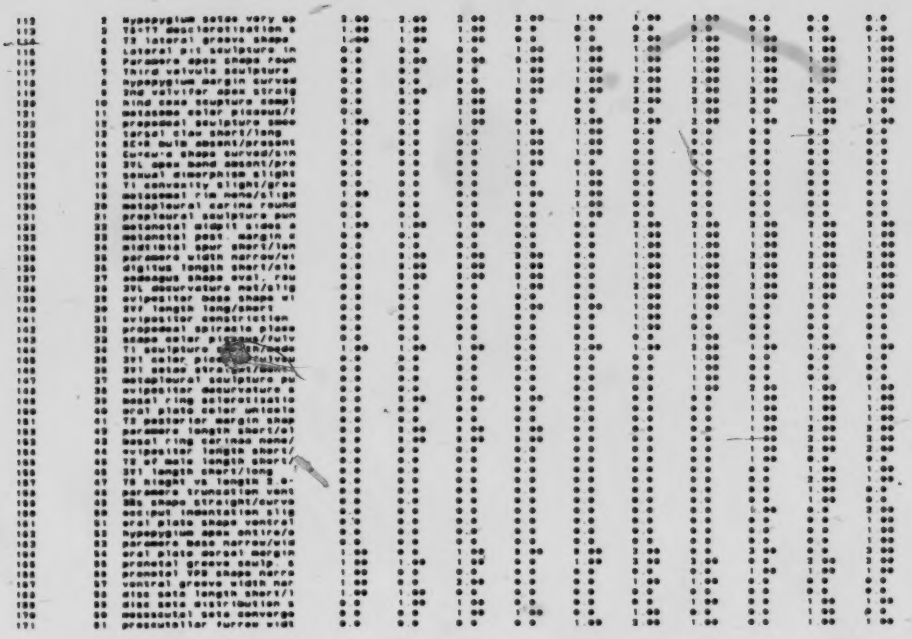
Summit Blaine Co. IDA. 15.VII.61 8600' B,H, Poole (CNC). Male, 3 females, Galena Summit, nr. Stanley, Ida. VIII.4,5.78 8700' H.&M. Townes (HT). Male, 8 females, nr. Stanley, Ida. Aug 3 1978 H.&M. Townes (HT). **Michigan**: Male, Crystal Falls VII or VIII.69 Mich. H.K. Townes (HT). Male, Female, Crawford Co. Mich. VII-10-59 R. and K. Dreisbach (USNM). **Minnesota**: Female, Gentilly Minn. July 12-14 1935 D.G. Denning (USNM). Female, U.S.A., Minnesota Clay Co. Buffalo River State Park Malaise Trap July 3 1973 (UM). 2 females, Moorhead Clay Co..Minnn. VI-23, 27-1972 J.R. Powers Collr. (UCB). 2 females, Washington Island, Basswood Lake, Lake Co., Minn. July 14, Aug. 14, 1950 R. Namba (USNM). **Montana**: Female, Butte, Montana August 4, 1921 F.M. Sallee (USNM). **Nevada**: Female, Angel L. NEVADA 12mi. SW. Wells 11.VII.61 8400' B.H. Poole (CNC). **New Mexico**: Female, Springer N.M. CN Ainslie Collector (USNM). Male, 8 females, Santa Fe NM Cockerell collector (USNM). **Oregon**: 2 males, 5 females, Pinehurst, Ore. June 23, 1978 H.&M. Townes (HT). 4 females, Ochoco Creek VII.8, 14.28 Ore. H.&M. Townes (HT). Male, 2 females, Hyatt Reservoir VI.25, 26, 30.78 H.&M. Townes (HT). Male, Seneca, Oregon July 11 1978 H.&M. Townes (HT). Male, 8 females, Seneca, Ore. VII-11, 24-35 Joe Schuh Coll. (OSU). 2 females, Summit Prairie, Ore. VIII-3-35 Joe Schuh Coll. (OSU). Male, (Keerins Ranch) Izee, Ore. VI-25-35 Joe Schuh Coll. (OSU). Male, Ore. Deschutes Co. Tumalo St. Pk. 27 June 1961 D.R. Smith (OSU). Female, Crater Lake Park, Ore. 8mi out Medford Rd. About 5500ft. elev. Aug. 10, 1930 H.A. Scullen, Coll. (OSU). Female, Meacham, Or. 3680ft. elev. July 19, 1929 H.A. Scullen, Coll (USNM). Male, female, Indian Ford, 3200' 6mi. NW. Sisters Deschutes Co. Ore. 10.VII.65 E.&I. Munroe (CNC). Female, 7mi. SW Beatty Klamath Co. Ore. VII-10-57 J.A. Powell Collector (UCB). **South Dakota**: Female, Whitewood, S.D. July 23-1924 (USNM). Male, female, 2mi. S. Sylvan L. Black Hills, S.D. VII.11.1961 H.&A. Howden (CNC). **Utah**: 4 females, Daniels Pass, UTAH 2mi. S. Wasatch Co. 9.VII.1961 8500' B.H. Poole (CNC). 3 males, Guardsman Pass, nr. Brighton UTAH 10.VII.1961 9,800' B.H. Poole summit (CNC). 2 females, 30mi. N. of Vernal, Utah 8400' VII.8.1961 Brian Poole (CNC). 2 males, female, Duck Creek Camp Utah Kane Co.

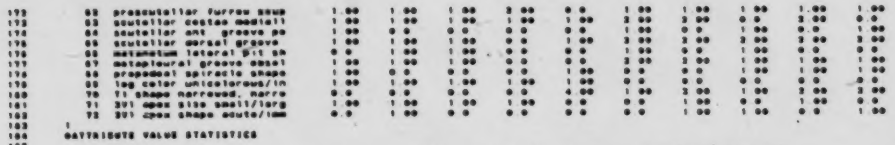
VII.11.1961 G.F. Knowlton Collector (USNM, UCD). Male, UTAH: Cache Co. Elk Valley 22 VIII 1976 G.F. Knowlton (USNM). Male, Cedar Breaks Iron Co. Utah VII-11 1961 G.F. Knowlton Collector (UCD). Female, Allens Cyn. Rich Co. Ut. VII.20-1962 G.F. Knowlton Collector (UCD). Female, Bear Canyon Mt. Nebo Ut. Juab Co. VIII.2-1962 G.F. Knowlton Collector (UCD). **Washington**: 2 males, 2 females, Mt. Rainier, Wash 2700ft, 5000' Jul. 8, VII.9 1940 H.&M. Townes (HT). 4 males, 7 females, Spokane, Wash. Sept. 74, Apr. 75 R. Oetting ex. Protagrotis obscura (USNM). Male, WASH: Oylmpic N.P. Dosewallips Rgr. Sta. VII-18-66 W. Gagne J Haddock collectors (JWC). Female, W.M. Mann Pullman Wash VII:17:08 (USNM). Female, Pullman Wash JA Hyslop Collector (USNM). Male, Uniontown Wash JM Aldrich Coll 6.26.32 (USNM). **Wyoming**: Female, Battle L. Road, Wyo. Sierra Madre Range 18.VII.1961 B.H. Poole (CNC). **Other**: Female, Wollah 6.8.88 (USNM).

12. APPENDIX 3. TAXMAP DATA FILE

4648







ATTRIBUTE VALUE STATISTICS

	ATTRIBUTE	TYPE	MAX	MIN	RANGE	INTRVL	CLASSES	LGDMT	FREQUENCIES BY CLASS									
									MS	1	2	3	4	5	6	7	8	9	10 >
10																			
	1 T3 ant margin curved/in	3	1.00	0.0	1.00	1.000	3.00	1.0000	2	6	3	0	0	0	0	0	0	0
	2 Hypopygium setae very sp	3	3.00	0.0	3.00	1.000	3.00	1.0000	0	3	3	4	0	0	0	0	0	0
	3 T2+T7 megalorotization s	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	7	3	0	0	0	0	0	0	0
	4 T3 lateral groove shape	3	2.00	0.0	2.00	1.000	3.00	1.0000	0	3	3	3	0	0	0	0	0	0
	5 Lateral pit sculpture in	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	3	7	0	0	0	0	0	0	0
	6 Paramere apex shape roun	3	1.00	0.0	1.00	1.000	2.00	1.0000	3	1	6	0	0	0	0	0	0	0
	7 Third valvula sculpture	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	3	7	0	0	0	0	0	0	0
	8 Hypopygium margin curved	3	3.00	0.0	3.00	1.000	3.00	1.0000	0	3	5	2	0	0	0	0	0	0
	9 2ND valvifer apex straig	5	5.00	0.0	5.00	1.000	5.00	2.3219	3	3	0	3	1	1	3	0	0	0
	10 Hind coxa sculpture compl	4	3.00	0.0	3.00	1.000	4.00	1.0000	0	4	1	1	0	0	0	0	0	0
	11 metacoxa color pleasou/f	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	7	3	0	0	0	0	0	0	0
	12 propodeal sculpture amou	3	3.00	0.0	3.00	1.000	4.00	1.0000	0	3	3	3	1	0	0	0	0	0
	13 tarsal claw short/long	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	3	0	0	0	0	0	0	0
	14 SC+R bulb absent/present	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	3	0	0	0	0	0	0	0
	15 Curvure shape curved/str	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	3	0	0	0	0	0	0	0
	16 3YL apex band absent/pre	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	1	0	0	0	0	0	0	0
	17 sexual dimorphism slight	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	1	0	0	0	0	0	0	0
	18 T1 convexity slight/grea	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	1	0	0	0	0	0	0	0
	19 metasomal rim none/sligh	3	2.00	0.0	2.00	1.000	3.00	1.0000	0	7	3	1	0	0	0	0	0	0
	20 metaplaural carina rounc	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	1	0	0	0	0	0	0	0
	21 preplaural sculpture pun	3	1.00	0.0	1.00	1.000	2.00	1.0000	0	4	1	0	0	0	0	0	0	0

```
210      32 metanotal midpit sides a   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  2  2  0  0  0  0  0  0  0
211
211      33 metanotal post  margin c   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  0  0  0  0  0  0  0  0
212
212      34 mtbtibial spur short/lon   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  0  0  0  0  0  0  0  0
213
213      35 paramere width narrow/wi   2  2.00  0.0   2.00  1.000    3.00 1 0.000   2  2  2  2  0  0  0  0  0  0
214
214      36 digitus length short/elo   2  2.00  0.0   2.00  1.000    3.00 1 0.000   2  2  2  2  0  0  0  0  0  0
215
215      37 aedeagus shape oval, rou   2  1.00  0.0   1.00  1.000    2.00 1 0.000   2  2  0  0  0  0  0  0  0  0
216
216      38 3V1 decurvature mes/stig   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  0  1  0  0  0  0  0  0  0
217
217      39 ovipositor base shape wi   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  0  0  0  0  0  0  0  0
218
218      30 3V7 length long/short      2  1.00  0.0   1.00  1.000    2.00 1 0.000   2  0  2  0  0  0  0  0  0  0
219
219      31 ovipositor constriction    2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
220
220      32 propodeal spiracle place   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
221
221      33 scape color piceous/fulv   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
222
222      34 T1 sculpture smooth/mode   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  1  7  2  0  0  0  0  0  0
223
223      35 3V1 color piceous/fulvou   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
224
224      36 3V1 setae straight/bent-   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
225
225      37 metapleural sculpture pu   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
226
226      38 ovipositor decurvature s   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  0  2  1  0  0  0  0  0  0
227
227      39 basal ring coloration/sc   2  1.00  0.0   1.00  1.000    2.00 1 0.000   2  4  2  0  0  0  0  0  0  0
228
228      40 oral plate color unicolo   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  7  2  0  0  0  0  0  0  0
229
229      41 T2 posterior margin shap   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  7  2  0  0  0  0  0  0  0
230
230      42 paramere length short/el   2  2.00  0.0   2.00  1.000    3.00 1 0.000   2  4  1  2  0  0  0  0  0  0
231
231      43 basal ring carinae none/   2  2.00  0.0   2.00  1.000    3.00 1 0.000   2  4  1  2  0  0  0  0  0  0
232
232      44 ovipositor length short/   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  7  1  2  0  0  0  0  0  0
233
233      45 T3 of male length short/   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
234
234      46 3V1 length short/long      2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  2  0  0  0  0  0  0  0
235
235      47 T3 height vs length 2 0-   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  0  1  1  0  0  0  0  0  0
236
236      48 paramere truncation vent   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
237
237      49 3Ba shape straight/curva   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
238
238      50 occiput incantation stig   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  0  1  1  0  0  0  0  0  0
239
239      51 oral plate shape ventral   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
240
240      52 hypopygium apex entire/e   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
241
241      53 paramere base narrow/wid   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  1  0  0  0  0  0  0  0
242
242      54 oral plate dorsal margin   3  3.00  0.0   3.00  1.000    4.00 1 0.000   2  2  2  1  2  0  0  0  0  0
243
243      55 pronotal groove sculp  s   3  3.00  0.0   3.00  1.000    4.00 1 0.000   0  2  4  2  2  0  0  0  0  0
244
244      56 pronotal tPS shape narro   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  4  0  0  0  0  0  0  0
245
245      57 ventral groove width nar   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  0  2  1  0  0  0  0  0  0
246
246      58 disc seta length short/l   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  2  0  0  0  0  0  0  0
247
247      59 disc seta distribution s   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  2  0  0  0  0  0  0  0
248
248      60 mesoscutal seta converge   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  4  0  0  0  0  0  0  0
249
249      61 prescutellar furrow widt   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  0  2  1  0  0  0  0  0  0
250
250      62 prescutellar furrow scup   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  1  2  1  0  0  0  0  0  0
251
251      63 scutellar costae medioll   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  2  0  2  0  0  0  0  0  0
252
252      64 scutellar ant  groove po   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  4  0  0  0  0  0  0  0
253
253      65 scutellar dorsal groove    2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  1  2  0  0  0  0  0  0  0
254
254      66 metanotum lateral pit sh   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  4  0  0  0  0  0  0  0
255
255      67 metapleural groove obsol   2  2.00  0.0   2.00  1.000    3.00 1 0.000   0  2  0  2  0  0  0  0  0  0
256
256      68 propodeal spiracle shape   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  2  0  0  0  0  0  0  0
257
257      69 leg color unicolorous/in   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  2  0  0  0  0  0  0  0
258
258      70 T1 shape narrowed, narro   2  4.00  0.0   4.00  1.000    6.00 2 3.010   0  0  2  2  1  1  0  0  0  0
259
259      71 3V1 apex size small/larg   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  4  0  0  0  0  0  0  0  0
260
260      72 3V1 apex shape acute/ima   2  1.00  0.0   1.00  1.000    2.00 1 0.000   0  0  4  0  0  0  0  0  0  0
261  ATTRIBUTES WEIGHTED BY CALCULATED INFORMATION  CAPACITY
262  APPROXIMITIES TO BE COMPUTED USING ATTRIBUTES   1 TO  72
263  APPROXIMITIES (AS DISTANCE * 1000), COMPUTED FOR ATTRIBUTES    1 TO  72
264        1  3 133   3 166   4 301   5 333   5 466   7 465   5 433   5 433  10 524   3  95   4 273   5 365   5 433   7 494   5
     416
265        2  5 466  10 499   6 393   5 416   5 366   7 426   5 443   5 426  10 513   5 367   5 426   7 502   5 466   5 494  10
     566
266        5  5 453   7 465   6 520   5 577  10 567   7 166   5 330   5 365  10 431   5 495   5 350  10 430   5 365  10 166  10
     302
267  NEAREST NEIGHBOURS (DISTANCE *1000)
268
269     1 latera   1 S. latera     1   3 133   1   3 166   1   4 301   1   5 333   1   5 466   1   5 426   1   7 465   1   5 4
     33
270     2 papiti   2 S  papiti     2   2  95   1   3 133   2   4 273   2   5 365   2   5 416   2   7 426   2   5 433   2   5 4
     54
271     3 eugeni   3 S  eugeni     3   2  95   1   3 166   3   4 303   3   5 330   3   5 416   3   7 426   3   5 426   3   5 4
     43
272     4 leovid   4 S  leovid     4   5 267   3   4 273   1   4 301   3   4 393   4   5 430   4   5 469   4   5 494   4   7 5
```

```
 5 appori   5 5  appori    4   5 357    1   5 373    2   5 388    3   5 410    5   5 452    6   7 486    6   8 520    6   8 5
 5 masoni   5 5  masoni    5   7 198    5   8 338    6   8 385    3   8 385    1   8 406    8  10 421    2   8 438    4   8 4
 7 cincti   7 5  cincti    5   7 198    7   8 368    7   8 406    2   7 424    3   7 424    7  10 438    1   7 455    5   7 6
 8 circum   8 5  circum    8  10 198    5   8 368    6   8 438    7   8 466    2   8 610    1   8 638    3   8 643    4   8 4
 9 moesmx   9 5  moesmx    5  10 202    8   8 368    7   8 368    6   8 385    3   8 424    2   8 454    1   8 455    4   8 4
10 falcat  10 5  falcat    8  10 198    9  10 202    6  10 421    7  10 438    3  10 499    3  10 519    1  10 524    4  10 5

                FREQUENCIES OF PROXIMITIES AT  01 INTERVALS
      DISTANCE  NO   TOTAL  REMAINDER  HISTOGRAM
        0 01     0     0       45
        0 02     0     0       45
        0 03     0     0       45
        0 04     0     0       45
        0 05     0     0       45
        0 06     0     0       45
        0 07     0     0       45
        0 08     0     0       45
        0 09     0     0       45
        0 10     1     1       44   .
        0 11     0     1       44
        0 12     0     1       44
        0 13     1     2       43   .
        0 14     0     2       43
        0 15     1     3       42   .
        0 16     0     3       42
        0 17     0     3       42
        0 18     0     3       42
        0 19     1     4       41   .
        0 20     1     5       40   .
        0 21     1     6       39   .
        0 22     0     6       39
        0 23     0     6       39
        0 24     0     6       39
        0 25     0     6       39
        0 26     0     6       39
        0 27     2     8       37   ..
        0 28     1     9       36   .
        0 29     1    10       35   .
        0 30     1    11       34   .
        0 31     0    11       34
        0 32     0    11       34
        0 33     1    12       33   .
        0 34     1    13       32   .
        0 35     0    13       32
        0 36     0    13       32
        0 37     1    14       31   .
        0 38     0    14       31
        0 39     3    17       28   ...
        0 40     0    17       28
        0 41     2    19       26   ..
        0 42     2    21       24   ..
        0 43     5    26       19   .....
        0 44     3    29       16   ...

        0 45     1    30       15   .
        0 46     2    32       13   ..
        0 47     3    35       10   ...
        0 48     0    35       10
        0 49     1    36        9   .
        0 50     2    38        7   ..

        0 51     1    39        6   .
        0 52     2    41        4   ..
        0 53     2    43        2   ..
        0 54     0    43        2
        0 55     0    43        2
        0 56     1    44        1   .
        0 57     0    44        1   .
        0 58     1    45        0   .
        0 59     0    45        0
        0 60     0    45        0
        0 61     0    45        0
        0 62     0    45        0
        0 63     0    45        0
        0 64     0    45        0
        0 65     0    45        0
        0 66     0    45        0
        0 67     0    45        0
        0 68     0    45        0
        0 69     0    45        0
        0 70     0    45        0
        0 71     0    45        0
        0 72     0    45        0
        0 73     0    45        0
        0 74     0    45        0
        0 75     0    45        0
        0 76     0    45        0
        0 77     0    45        0
        0 78     0    45        0
        0 79     0    45        0
        0 80     0    45        0
        0 81     0    45        0
        0 82     0    45        0
        0 83     0    45        0
        0 84     0    45        0
        0 85     0    45        0
        0 86     0    45        0
        0 87     0    45        0
        0 88     0    45        0
        0 89     0    45        0
        0 90     0    45        0
        0 91     0    45        0
        0 92     0    45        0
        0 93     0    45        0
        0 94     0    45        0
        0 95     0    45        0
        0 96     0    45        0
        0 97     0    45        0
        0 98     0    45        0
        0 99     0    45        0
        1 00     0    45        0

    1   MAP CLUSTER ANALYSIS -Morphological characters of Sothon species

        OTU LISTED AFTER BLANK LINE IS EXCLUDED FROM CLUSTER FOR REASON(S) INDICATED BY FLAG
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```
388            FLAG 1 = AVERAGE LINKAGE CRITERION EXCEEDED. FLAG 2 = SINGLE LINKAGE CRITERION EXCEEDED.
387            FLAG 3 = RATIO CRITERION VIOLATED. FLAG 4 = OTU ALREADY IN A CLUSTER
386
385            (MAXIMUM NUCLEUS 0.187. MAXIMUM RISE 0.0438 BOTH ARE 100% OF NORMAL)
384            ATTRIBUTES WEIGHTED BY CALCULATED INFORMATION CAPACITY
383
382  0         CLUS OTU DIST OTU  AVEDF  RISE FAR DIST FLAG NAME OF OTU
381            TER  NOS BEST BEST  NEW     IN  OTU FAR
380            NO       LINK LINK LINKS  AVE      OTU
379            ------------------------------------------------------------
378              1   2                                        papilli   2 S  papillomas
377                  2 0.10                                   augoni    2 S  augoni
376                  1 0.12     2 0.135 0.037    3 0.15       latoria   1 S  latorallis
375
374                4 0.27     3 0.383 0.148    3 0.20 1200 leovid    4 S  leovidorbus
373            ------------------------------------------------------------
372  0         ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)
371
370            CLUSTER OTU LABEL
369                 3   4 leovid    4 S  leovidorbus
368                 3   5 aggori    5 S  aggoris
367                 4   6 masoni    6 S  masoni
366                 5   7 cincti    7 S  cinctiformis
365                 5   8 circum    8 S  circumflexus
364                 7   9 nasmax    9 S  nasmaximus
363                 8  10 falcat   10 S  falcatus
362  0         CLUSTER MEMBERSHIP INDEX
361
360               1   1
359               2   1
358               3   1
357               4   2
356               5   3
355               6   4
354               7   5
353               8   6
352               9   7
351              10   8
350  1    HAPPINE AIDS
349       ------------
348
347  0    CENTRALITY-PERIPHERALITY ORDER
346       OTU'S      6   2   7   3   1   8   4   9  10   5
345       CLUSTERS   4   1   5   1   1   6   2   7   6   3
344  0    CLUSTER DISTANCES (*1000)
343            MAIN DIAGONAL = CLUSTER RADII (I.E. 1/2 THE DISTANCE BETWEEN
342                  THE TWO MOST DISTANT OTUS IN THE CLUSTER)
341            LOWER TRIANGLE = CENTER TO CENTER DISTANCES OF CLUSTER CIRCLES
340                 (I.E. RADIUS 'A' + RADIUS 'B' + DISTANCE BETWEEN NEAREST NEIGHBORS IN A AND B)
339            UPPER TRIANGLE = MINIMUM INTER-CLUSTER DISCONTINUITIES
338                 (I.E., DISTANCE BETWEEN NEAREST NEIGHBORS IN A AND B)
337  0CLUSTER        1         2         3         4         5         6         7         8
336       1        73       272       323       388       424       414       424       496
335       2       345         0       267       435       502       480       494       559
334       3       388       267         0       453       486       523       577       601
333       4       458       435       453         0       198       330       388       431
332       5       487       502       486       198         0       406       359       438
331       6       487       480       439       330       406         0       388       185
330       7       457       494       577       388       359       388         0       302
329       8       583       559       587       431       438       185       302         0
```

```
328  !ATTRIBUTES EQUALLY WEIGHTED Morphological characters of Salmon species
327  0PROXIMITIES TO BE COMPUTED USING ATTRIBUTES    1 TO   73
326  0PROXIMITIES (AS DISTANCE * 1000), COMPUTED FOR ATTRIBUTES    1 TO   73
325       1   2 133   3 158   4 297   5 333   6 434   7 440   8 485  10 530   3 103   4 292   5 303   6 434   7 434   8
     431
     2
     557
324       9 471  10 494   4 297   5 430   6 303   7 434   8 457   9 425  10 530   5 243   6 415   7 462   8 485   9 462  10
     557
323       6 452   7 461   8 515   9 573  10 580   7 217   8 331   9 399  10 430   8 408   9 399  10 438   9 303  10 158  10
     215
322  0NEAREST NEIGHBOURS (DISTANCE *1000)
321
320       1 latora    1 S  latora     1   2 133     1   3 158     1   4 297     1   5 333     1   6 434     1   8 440     1   7 440     1   9 4
     95
319       2 papilli   2 S  papilli     2   3 103     1   2 133     3   4 292     2   5 303     2   6 431     2   7 434     2   8 434     2   9 4
     71
318       3 augoni    3 S  augoni      2   3 103     1   3 158     3   4 297     3   5 303     3   6 430     3   7 434     3   8 434     3   9 4
     57
317       4 leovid    4 S  leovid      4   5 243     2   4 292     1   4 297     4   5 415     4   6 415     4   7 462     4   8 4     4   9 4
     83
316       5 aggori    5 S  aggori      4   5 243     1   5 333     3   5 303     3   6 430     5   6 453     5   7 461     5   8 515     5   9 5
     73
315       6 masoni    6 S  masoni      8   7 217     8   8 331     8   9 399     3   6 303     4   6 415     6  10 430     1   6 430     3   9 4
     34
314       7 cincti    7 S  cincti      8   7 217     7   8 359     7   9 408     3   7 434     2   7 434     7  10 438     1   7 440     5   7 4
     61
313       8 circum    8 S  circum      8  10 158     8   8 303     8   9 331     7   8 408     3   8 431     1   8 440     3   8 457     4   8 4
     58
312       9 nasmax    9 S  nasmax      8  10 215     8   8 303     7   9 399     8   9 399     3   9 438     2   9 471     4   9 483     1   9 4
     95
311      10 falcat   10 S  falcat      8  10 158     9  10 215     8  10 430     7  10 438     3  10 494     1  10 530     3  10 539     4  10 5
     57
310  !              FREQUENCIES OF PROXIMITIES AT .01 INTERVALS
309  0          DISTANCE  NO     TOTAL  REMAINDER  HISTOGRAM
308
307                0 01       0       0        66
306                0 02       0       0        66
305                0 03       0       0        66
304                0 04       0       0        66
303                0 05       0       0        66
302                0 06       0       0        66
301                0 07       0       0        66
300                0 08       0       0        66
299                0 09       0       0        66
298                0 10       0       0        66
297                0 11       1       1        66  *
296                0 12       0       1        66
295                0 13       0       1        66
294                0 14       1       2        65  *
293                0 15       0       2        65
292                0 16       0       2        65
291                0 17       1       3        65  *
290                0 18       0       3        65
289                0 19       1       4        61  *
288                0 20       0       4        61
287                0 21       0       4        61
286                0 22       2       6        59  **
285                0 23       0       6        59
284                0 24       0       6        59
283                0 25       1       7        58  *
282                0 30       0       7        58
```

```
OTU'S      6   7   2   8   1   3   4   9  10   5
CLUSTERS   4   5   1   6   1   1   3   7   8   3
CLUSTER DISTANCES (*1000)
     MAIN DIAGONAL = CLUSTER RADII (1/2 THE DISTANCE BETWEEN
                     THE TWO MOST DISTANT OTUS IN THE CLUSTER)
     LOWER TRIANGLE = CENTER TO CENTER DISTANCES OF CLUSTER CIRCLES
                      (1/2 RADIUS 'A' + RADIUS 'B' + DISTANCE BETWEEN NEAREST NEIGHBORS IN A AND B)
     UPPER TRIANGLE = MINIMUM INTER-CLUSTER DISCONTINUITIES
                      (1/2 DISTANCE BETWEEN NEAREST NEIGHBORS IN A AND B)

OCLUSTER      1       2       3       4       5       6       7       8
    1        89     382     333     393     434     421     425     400
    2       376       0     243     416     482     488     483     557
    3       417     243       0     462     481     518     573     530
    4       473     416     462       0     217     321     390     430
    5       508     482     481     217       0     400     368     436
    6       506     488     518     321     400       0     353     186
    7       510     483     573     390     368     353       0     215
    8       479     557     530     430     436     186     215       0
```